Albian angiosperm pollen from shallow marine strata in the Lusitanian Basin, Portugal

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Research papers

Albian angiosperm pollen from shallow marine strata in the Lusitanian Basin, Portugal

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ABSTRACT

The evolution of angiosperms significantly changed the composition of the terrestrial vegetation during the mid-Cretaceous. In contrast to the wealth of information available on the biology and systematic relationships of early angiosperms, the temporal patterns of their evolution and radiation are poorly constrained. Here we present a continuous angiosperm pollen record from well-dated shallow marine deposits in the Lusitanian Basin, Portugal. The São Julião section provides a solid stratigraphic framework to track angiosperm pollen distribution patterns from the early Albian to early Cenomanian at mid-latitudes. In comparison to previous angiosperm pollen records from the Lusitanian basin, the section shows an extended late Albian succession and provides new insights into the diversification of early angiosperms during this important interval. Productive palynological samples were analysed and 79 different angiosperm pollen types have been recorded. Throughout the Albian angiosperm pollen represent only a minor component of the total palynoflora. The early Albian pollen record is characterized by highly diverse assemblages of monoaperturate pollen of monocot or "magnoliid" affinity and by the first appearance of polyporate and tricolpate pollen of eudicot affinity. A distinct diversification phase among tri- and poly-aperturate pollen (e.g., *Cretacaeiporites*, *Retitrescolpites*, *Rousea*, *Striatopollis* and *Tricolpites*) and the presence of conspicuous pollen grains assigned to *Dichastopollenites* characterize the middle and late Albian palynological assemblages. Thus, the section records a striking sequence of appearances of important angiosperm pollen morphologies. Monocolpates, polyporates and tricolpates appear in the early Albian whereas tricolporates appear from the early part of the late Albian onwards. Furthermore, well-constrained biostratigraphic ranges of selected angiosperm pollen from mid-latitudes are presented. In view of these new data, the temporal framework of the palynological Subzones II-B and II-C in the Potomac Group succession from the Atlantic Coastal Plain, eastern USA is revised to a middle to late Albian age.

1. Introduction

Mid-Cretaceous floras are characterized by the diversification and radiation of early angiosperms coinciding with a dramatic drop in the diversity of many gymnosperm and pteridophyte lineages (Lidgard and Crane, 1988, 1990; Crane and Lidgard, 1989; Crane et al., 1995). The oldest widely accepted angiosperm remains consist of rare monocolpate pollen (*Clavatipollenites*) of Valanginian age (Gübeli et al., 1984; Hughes and McDougall, 1987; Hughes, 1994). Angiosperms appeared in the lower latitudes and spread diachronously to higher latitudes. In most ecosystems angiosperms dominated the vegetation by the end of the Late Cretaceous (Lidgard and Crane, 1988; Crane and Lidgard, 1989). The oldest tri-aperturate pollen of eudicot affinity are recorded from the Barremian–Aptian of lower latitudes (Doyle et al., 1977; Penny, 1986, 1988; Regali and Viana, 1989; Schrank and Mahmoud, 2002; Ibrahim, 2002; Heimhofer and Hochuli, 2010), and from the Albian onwards in middle latitudes (Doyle and Robbins, 1977; Heimhofer et al., 2007).

The Lusitanian Basin represents an excellent study area to track early angiosperm radiation patterns during the mid-Cretaceous. Here, important angiosperm meso- and macrofossil remains, including reproductive organs, leaves, fruits and seeds have been described (Saporta, 1894; Teixeira, 1948; Groot and Groot, 1962; Friis and

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Pedersen, 2011; Friis et al., 1994, 1997, 1999, 2000a, 2000b, 2001, 2009, 2010, 2011; Mendes et al., 2011, 2014a, 2014b). The Potomac Group succession (Atlantic Coastal Plain, eastern USA) represents another classically important angiosperm pollen archive from the mid-Cretaceous (Brenner, 1963; Doyle, 1992). The compilation of Doyle and Robbins (1977) from the continental succession was used to demonstrate the continuous changes in angiosperm pollen morphology and evolution from the Aptian to Cenomanian. Due to the absence of adequate biostratigraphic marker species or radiometric dating these deposits lack independent time control.

In contrast, shallow marine strata provide an excellent archive for studying angiosperm pollen distribution patterns. The stratigraphic assignment of shallow marine deposits has been improved significantly by the use of strontium-isotope stratigraphy in low-Mg calcite fossils (e.g., oysters, rudists), dinoflagellate cyst biostratigraphy, and age-diagnostic ammonites and rudists. A continuous pollen record with well-constrained stratigraphic age control can be established, given that preservation is good and does not change throughout the studied succession. So far, two shallow marine sections from Portugal (Luz and Cresmina) provided a composite record to track the angiosperm pollen evolution between the late Barremian and the early late Albian (Heimhofer et al., 2007, 2012). The late Albian (107.7–100.5 Ma) represents a long interval of the Albian period (113–100.5 Ma) (Gradstein et al., 2012). However, until now this interval has not been adequately covered by palynological studies from the Lusitanian Basin (Heimhofer et al., 2005, 2007).

Here we present a high-resolution angiosperm pollen record from the independently dated shallow marine São Julião section in the Lusitanian Basin. This section covers strata of early Albian to early Cenomanian age with a significantly expanded late Albian succession and documents the distribution pattern of angiosperm pollen during an important but poorly documented phase in the early radiation of angiosperms.

The aim of this study is four-fold:

(1) Provide a continuous and high-resolution angiosperm pollen record from a stratigraphically calibrated succession in the Lusitanian Basin.
(2) Extend the existing angiosperm pollen record into the late Albian and early Cenomanian.
(3) Provide biostratigraphic age-ranges for selected angiosperm pollen species and morphological groups.
(4) Compare the stratigraphic angiosperm pollen succession from São Julião with the existing zonation based on the Potomac Group succession.

2. Geological setting

The São Julião section (section part I) is located in the Lusitanian Basin, 5 km south of the town of Ericeira (base location: N38°55′847″, W9°25′241″). The stratigraphic section with a total thickness of 192 m stretches for 3 km with a dip of 2° to the south and is easily accessible along the beach (Fig. 1). A detailed description of the São Julião outcrop is provided by Horikx et al. (2014). Due to unfavourable sampling conditions at the São Julião locality, the topmost 12 m of the composite section was sampled at a different locality 2 km further south (São Julião section part II).

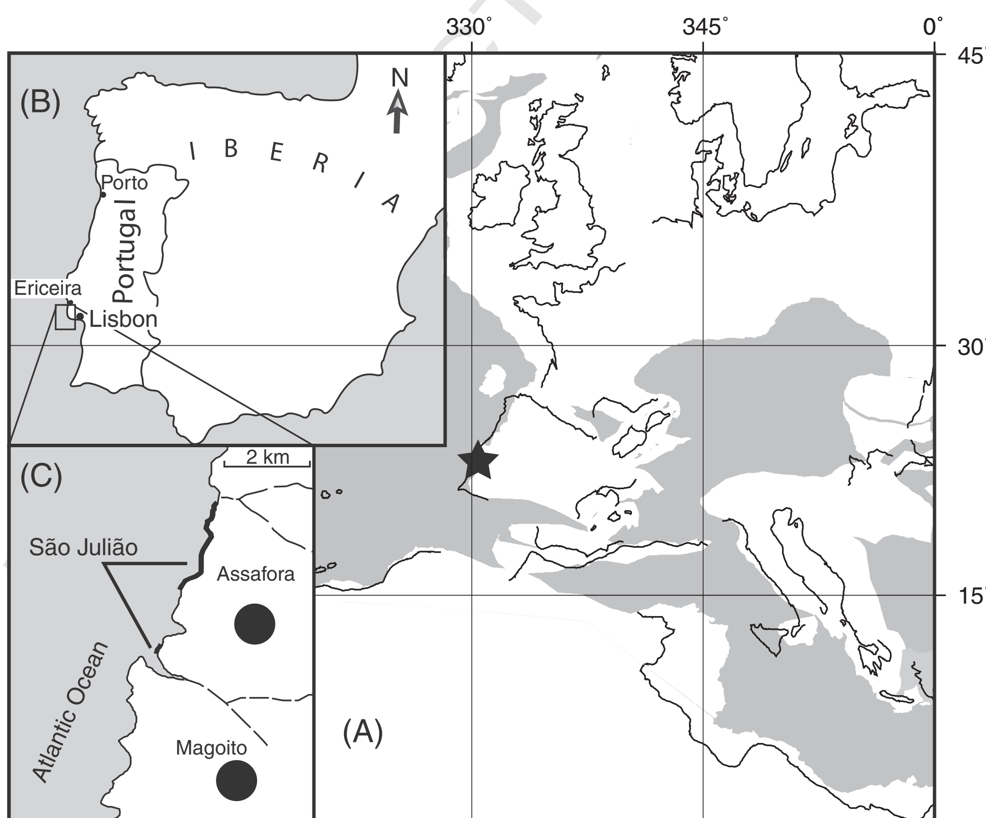

Fig. 1. (A) Palaeogeographic map for the Albian (105 Ma) and location of the São Julião section. (Map generated at http://www.odsn.de/odsn/services/paleomap/paleomap.html). (B) Location of the studied section on the Iberian Peninsula near the town of Ericeira. (C) Map of the study area showing the location of the coastal São Julião section (section part I and II, thick black lines) close to the villages of Assafora and Magoito, ca. 5 km south of Ericeira.

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2.1. Lithostratigraphy and sedimentological evolution

The Lusitanian Basin is located in the westernmost part of the Iberian Peninsula and filled with Mesozoic strata deposited on a passive continental margin. During the mid-Cretaceous the Lusitanian Basin was positioned at a palaeolatitude of about 25°N (Stampfli and Borel, 2002; Fig. 1). During the Early Cretaceous, deposition of fluvial and shallow marine sediments was confined to the central and southern part of the Lusitanian Basin. A sea level rise during the Valanginian–Barremian led to the deposition of more open marine strata (Rey,

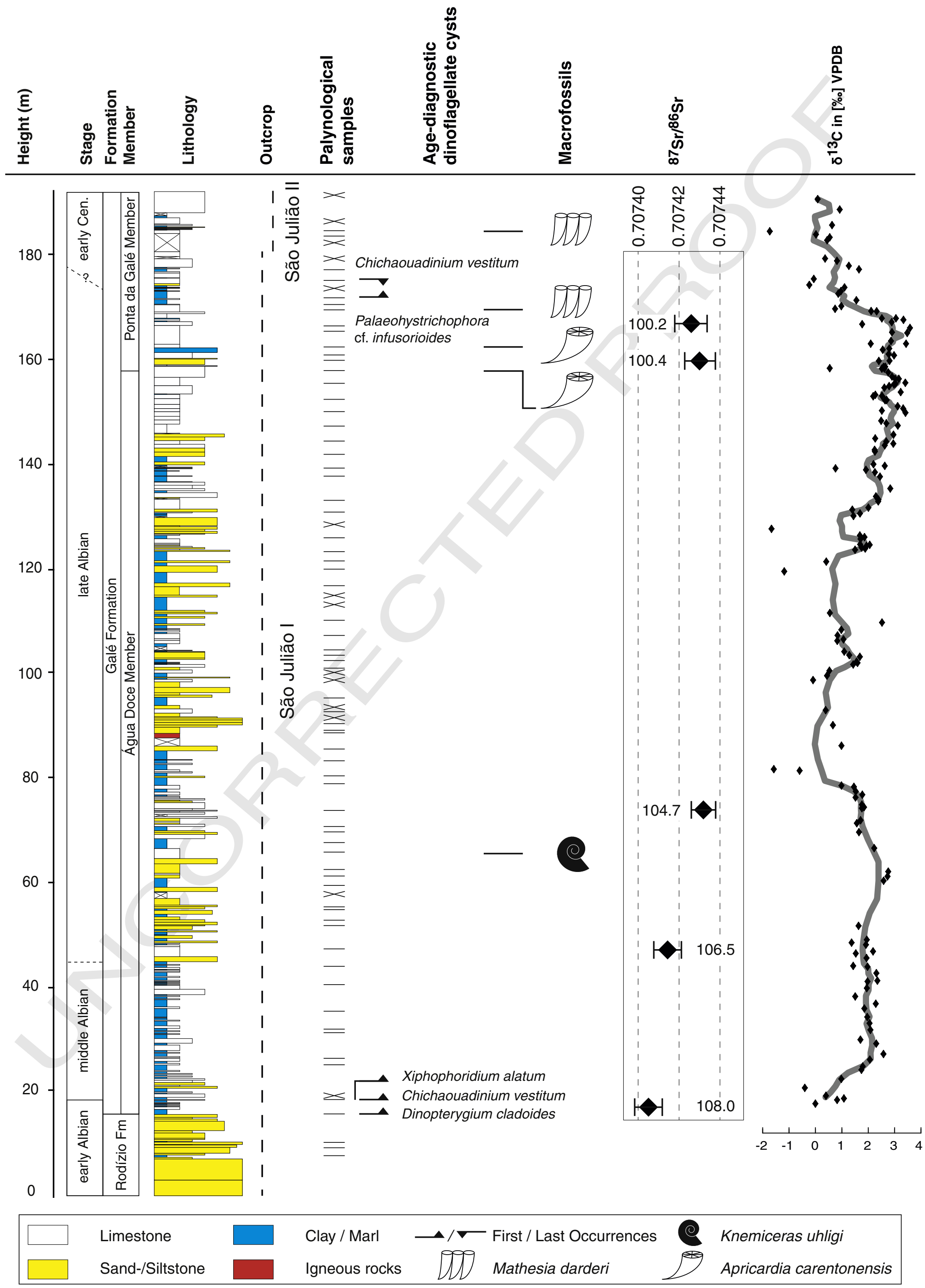

Fig. 2. Lithological log and age assignment of the São Julião section with the first and last occurrences of age-diagnostic dinoflagellate cysts and the position of biostratigraphically important macrofossils. Lines indicate the position of palynological samples, crosses indicate barren samples. Carbon-isotope record and strontium-isotope derived numerical ages with 2σ error bars measured on pristine oyster and rudist shells after Horikx et al. (2014). Lithological units follow Rey (1992).

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1979; Cunha and Pena dos Reis, 1995; Dinis et al., 2008). A break in sedimentation, related to the anti-clockwise rotation of Iberia during the Aptian–Albian transition, is expressed by a major unconformity (MU), well-known from large parts of the Lusitanian Basin (Dinis and Trincão, 1995; Dinis et al., 2002). After this phase of non-deposition and/or erosion, coarse-grained siliciclastic sediments with cross-bedded sands and conglomerates (Rodízio Formation) were deposited diachronously across the southern Lusitanian Basin (Dinis and Trincão, 1995; Rey et al., 2006; Dinis et al., 2008). At São Julião, the lowermost outcropping beds (0–16 m) correspond to the topmost part of the Rodízio Formation (Fig. 2). These fluvio-deltaic sediments are overlain by near-shore marine strata of the Galé Formation. According to Rey (1992) the Galé Formation can be subdivided into two lithological units, the lower Água Doce Member and the upper Ponta da Galé Member, respectively. The Água Doce Member (16–158 m) is composed of alternating thin (often sub-metre scale), shallow marine sandstone and sand-rich limestone beds with interbedded marls and clays, indicating variations in detrital input (Horikx et al., 2014). A shallow marine depositional setting for the Água Doce Member is corroborated by the common occurrences of bivalve and gastropod remains and the high content of opaque phytoclasts, plant-derived membranes, cuticles and terrestrial palynomorphs in palynological samples. The first occurrence (FO) of macroscopic rudist remains marks the base of the overlying Ponta da Galé Member (158–192 m; Rey, 1992). This member consists of thick rudist-rich limestone beds with intercalated orbitolinid-rich marls and variegated claystones. The top of the section is marked by the presence of a conspicuous, about 4 m thick pale-coloured sandy limestone bed rich in orbitolinids, which serves as a regional marker bed (D1 of Berthou and Lauverjat, 1979).

2.2. Integrated stratigraphy of the São Julião section

Throughout the São Julião section, typical Early Cretaceous marker fossils (e.g., ammonites, calcareous nannoplankton, planktonic foraminifera) are almost absent and stratigraphic age-assignments of these strata were based on bio- and lithostratigraphic correlations with more open marine strata (e.g., Berthou et al., 1980, Hasenboehler, 1981, Médus, 1982, Berthou, 1984). Recently the section was dated by dinoflagellate cyst biostratigraphy, strontium-isotope ratios from pristine low-Mg calcite oyster or rudist shells, as well as carbon-isotope chemostratigraphy (Horikx et al., 2014; Fig. 2). At São Julião, the lowermost 16 m is devoid of age-diagnostic dinoflagellate cysts, oysters and rudist shells. According to Heimhofer et al. (2007) the Rodízio Formation deposited above the MU throughout the Lusitanian Basin is of post-Aptian age. Evidence for an early Albian age is derived from the FO of the dinoflagellate cyst *Dinopterygium cladoides* (Monteil and Foucher, 1998 and Fig. 2) slightly above the base of the lowermost Água Doce Member. The FO of the typical middle Albian dinoflagellates *Xiphophoridium alatum* and *Chichaouadinium vestitum* (Monteil and Foucher, 1998), as well as strontium-isotope derived numerical ages place the early-middle Albian boundary at ~18 m (Horikx et al., 2014). Age diagnostic dinoflagellate cysts characteristic of the middle to late Albian boundary are absent. Based on Sr-isotope data and the presence of the ammonite *Knemiceras uhligi* of late Albian age, this boundary is placed at ~44 m (Horikx et al., 2014). The presence of the rudists *Apricardia carentonensis* and *Mathesia darderi* between 158 and 184 m supports a late Albian age (Horikx et al., 2014). *Apricardia carentonensis* has been reported from the late Albian to early Cenomanian (Berthou et al., 1979) and *M. darderi* was reported from the late Albian in Spain (Masse et al., 1998). The Albian–Cenomanian boundary is tentatively placed between 165 and 175 m in the uppermost part of the section based on the FO of *Palaeohystrichophora* cf. *infusorioides* and the disappearance of *C. vestitum* (Foucher, 1981; Williams et al., 2004), combined with strontium-isotope derived numerical ages (Horikx et al., 2014). This overall age of the São Julião record further supported the correlation of the carbon-isotope trend with other stratigraphically well-constrained marine sections in the Lusitanian Basin (Portugal), the Umbria-Marche Basin (Italy) and the Vocontian Trough (France) (Horikx et al., 2014 and references therein).

3. Material and methods

The section was logged bed-by-bed during two field campaigns in 2012 and 2013. Palynological samples were taken from various lithologies (claystones, marl, sandstones and limestones). In order to minimize the risk of contamination, samples from soft lithologies were taken after removal of the surficial scree. In total, 82 sediment samples were selected for palynological analyses. All samples were cleaned and dried for 24 h at 40 °C. Between 10 to 30 g of sample material was sent to the Geological Survey of Nordrhein-Westfalen in Krefeld, Germany for palynological preparation. In order to remove carbonates and silicates, samples were treated with HCl and HF following standard procedures (Traverse, 2007). Polyvinyl alcohol was used as the mounting medium and embedded by Elvacite 2044TM epoxy resin. From each of the 68 productive samples, two palynological strew mounts were prepared and analysed for their palynological content, with a particular focus on angiosperm pollen. The quality of preservation of the palynomorphs is good to excellent as indicated by the preservation of delicate, fine sculptured and thin-walled (angiosperm) pollen and the generally low frequency of damaged palynomorphs. Samples were studied with an OLYMPUS BX 53 transmitted light microscope using a 100× oil immersion objective and differential interference contrast. The presence/absence diagram of the angiosperm pollen in the productive samples was plotted using the Tilia software of Grimm (1991). Light photomicrographs were taken with an OLYMPUS XC 50 digital camera. All slides and remaining palynomorph residues are stored at the Institute for Geology in Hanover, Germany. In order to identify and exclude contamination by modern pollen, suspicious pollen grains were analysed under fluorescence light using an X-Cite 120Q light source. Cretaceous angiosperm pollen grains emit distinctly less fluorescence than modern pollen, or no fluorescence at all, and can be readily distinguished from potential modern contamination. A selection of the described angiosperm pollen grains was analysed using confocal laser scanning microscopy (CLSM) at the Biology Department of the Technische Universität Darmstadt, Germany. CLSM provides high resolution, fluorescence images of optical sections through an embedded specimen and is applicable to standard palynological slides without any further sample preparation. Optical sections were captured with an image resolution of 1024 × 1024 pixels and a distance between sections of less than 400 nm. Stacking the optical sections provided a three-dimensional view, with a much higher resolution and depth of field than in normal light microscopy (LM). Confocal images were taken on a Leica TCS_SP under oil immersion at an excitation wavelength of 488 nm and detection of emitted fluorescence light at 500 nm and longer.

4. Results

The São Julião section contains rich assemblages of well-preserved angiosperm pollen. In total, 79 different angiosperm pollen species were distinguished. The majority of these pollen grains (49 taxa) are of eudicot affinity (Fig. 3), whereas 30 different monocolpate pollen taxa of monocot or “magnoliid” affinity (which includes members of the magnoliid clade, the basal ANITA lines, and Chloranthaceae) were observed. Angiosperm pollen grains are illustrated on Plates I–VIII and comprehensive

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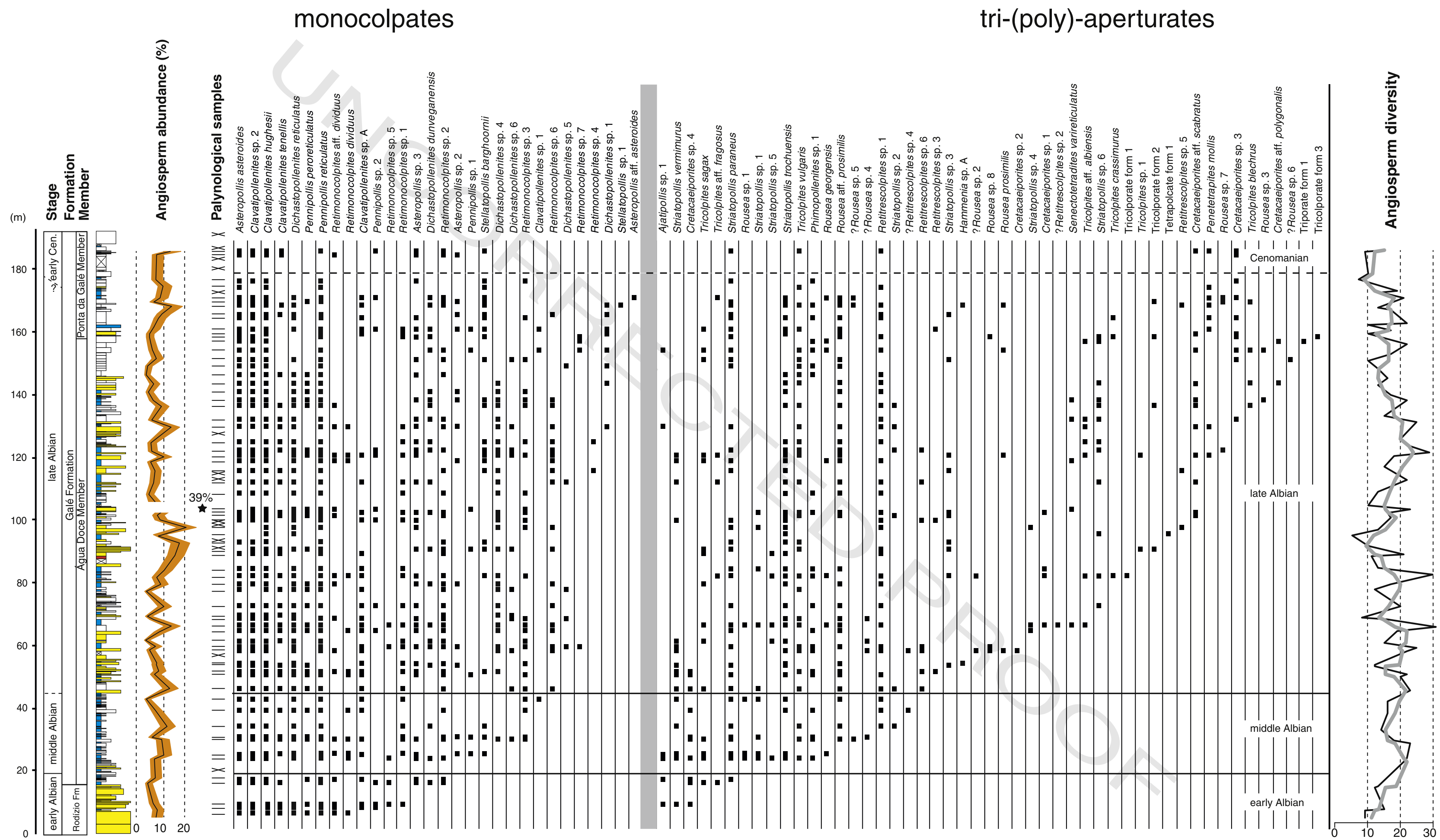

Fig. 3. Relative angiosperm pollen abundances of the total spore-pollen assemblage and stratigraphic distribution of angiosperm pollen in the São Julião section plotted against lithology and age. Orange shading indicates the 95% confidence interval. Horizontal lines indicate position of the productive samples, crosses indicate barren palynological samples. Angiosperm diversity represents the number of taxa per sample, grey line represents three-point moving average.

morphological descriptions of the different pollen species are provided in Appendix 1. The pollen grains were differentiated based on important morphological characteristics including size, shape and aperture configuration, exine structure and surface patterns such as ornamentation type, e.g., size and shape of the lumen and muri.

4.1. Systematic palynology

The recovered angiosperm pollen grains were compared with previously published records and – if possible – assigned to established taxa. However, numerous pollen grains from the São Julião record have not been described or differ significantly from previously published records and are catalogued as informal species.

Genus *Ajatipollis* Krutzsch 1970

Description and botanical affinity:
Tetrahedral tetrads of triporate pollen, amb of the individual grains circular to subcircular, 10–13 µm in diameter, diameter of tetrad 21–23 µm. Pores are arranged along the equator of the individual grains and grouped in clusters of three pores (Garside's law) (Krutzsch, 1970). Structure semitectate, columellate; the columellae are very densely spaced and fused at their heads forming a perforate tectum. *Ajatipollis* sp. 1 differs from the type species (Krutzsch, 1970) by its large pores (5–6 µm) and thick (2 µm) exine.
Recorded species: (for description see Appendix 1).
Ajatipollis sp. 1, Plate I, 1–2.

Genus *Asteropollis* Hedlund and Norris 1968

Description and botanical affinity:
Monocolpate pollen grains with short 3- to 6-branched colpus (tri- to hexachotomocolpate) with branches almost reaching the equatorial region of the grain, amb circular to sub-circular, 14–28 µm in diameter. Structure semitectate, columellate; in some species the columellae are very densely spaced with fused heads forming a perforate tectum. In contrast to the original description of *Asteropollis* described as having more a more than three-armed sulcus (Hedlund and Norris, 1968), trichotomocolpate pollen grains are here also included in *Asteropollis*, following Heimhofer et al. (2007). The exine structure and 4- to 5-branched colpus of several *Asteropollis* pollen types are similar to extant *Hedyosmum* pollen of the Chloranthaceae family (Doyle, 1969; Walker and Walker, 1984; Eklund et al., 2004; Doyle and Endress, 2014).
Recorded species: (for descriptions see Appendix 1).
Asteropollis asteroides, Plate I, 3–4.
Asteropollis aff. *asteroides*, Plate I, 5–6. This form differs from *Asteropollis asteroides* (Hedlund and Norris, 1968) by its 6-branched colpus (hexachotomocolpate).
Asteropollis sp. 2 sensu Heimhofer et al. (2007), Plate I, 8–9.
Asteropollis sp. 3 sensu Heimhofer et al. (2007), Plate I, 7.

Genus *Clavatipollenites* Couper 1958

Description and botanical affinity:
Monocolpate pollen grains with broad and elongate sometimes indistinct colpus, amb elliptical to circular, long axis 14–35 µm. Structure semitectate, columellate; in some specimens the columellae are very densely spaced and fused at their heads forming a perforate tectum. Detailed analysis on exine structure and the presence of in-situ pollen in fossil reproductive structures place *Clavatipollenites* within the extant Chloranthaceae family (Couper, 1953; Walker and Walker, 1984; Archangelsky and Archangelsky, 2013). However, the exact position of *Clavatipollenites* within Chloranthaceae is questioned. A close comparison of fossil fruits (*Couperites*) containing in-situ *Clavatipollenites* to modern Chloranthaceae fruits, places *Clavatipollenites* outside the extant family of Chloranthaceae (Pedersen et al., 1991). Likewise Doyle and Endress (2014) obtained ambiguous results for the exact position of *Couperites* in their phylogenetic analysis and argued that not all pollen assigned to *Clavatipollenites* are related to Chloranthaceae. According to other sources, *Clavatipollenites* shows strong similarities to the pollen of *Austrobaileya* (Endress and Honegger, 1980) and *Trimenia* (Sampson and Endress, 1984).
Recorded species: (for descriptions see Appendix 1).
Clavatipollenites sp. A sensu Doyle and Robbins (1977), Plate I, 10–11.
Clavatipollenites hughesii, Plate I, 14–15.
Clavatipollenites sp. 1, Plate I, 12–13.
Clavatipollenites sp. 2 sensu Heimhofer et al. (2007), Plate I, 16.
Clavatipollenites tenellis, Plate II, 1–2.

Genus *Cretacaeiporites* Herngreen 1973

Description and botanical affinity:
Pollen grains with multiple (more than three) scattered pores, diameter of the pores 1.0–4.0 µm. Amb circular to sub-circular, 17–25 µm in diameter. Exine semitectate, striato-reticulate or reticulate-semitectate, columellate; reticulum homobrochate or heterobrochate; lumen diameter 0.5–2.5 µm, irregularly shaped. In some species overtopping columellae form a verrucate surface on the muri. Due to the wide range of pollen morphologies among *Cretacaeiporites*, the exact botanical affinity remains unclear. The exine structure of one species of *Cretacaeiporites* was studied with SEM and TEM by Ward and Doyle (1994) with inconclusive results.
Recorded species: (for descriptions see Appendix 1).
Cretacaeiporites aff. *polygonalis*, Plate II, 3. This form differs from *Cretacaeiporites polygonalis* (Herngreen, 1973) by its scabrate to granulate exine structure as seen under light microscope.
Cretacaeiporites aff. *scabratus*, Plate II, 4. This form differs from *Cretacaeiporites scabratus* (Herngreen, 1973) by the smaller pore size (<1 µm).
Cretacaeiporites sp. 1, Plate II, 5–6.
Cretacaeiporites sp. 2, Plate II, 7–9.
Cretacaeiporites sp. 3, Plate II, 10–11.
Cretacaeiporites sp. 4, Plate II, 12–13.

Genus *Dichastopollenites* May 1975

Description and botanical affinity:
Zonosulcate pollen grains, colpus separates the grains equatorially into two hemispheres, amb circular to elliptical, 20–50 µm in diameter. Structure reticulate-semitectate; reticulum homobrochate or heterobrochate; lumen diameter 1.0–12.0 µm; muri width 0.3–1.4 µm. In some forms the meandering muri and lumen form an irregular reticulum 'maze' structure, in other forms the reticulum is composed of small lumen adjacent to larger lumen. In some forms the muri surface is verrucate because of overtopping columellae. *Dichastopollenites* pollen have been compared to extant Nymphaeaceae (May, 1975). However, in-situ pollen found on the surface of fossil Nymphaeales flowers are remarkably different from *Dichastopollenites* and question a direct affinity of *Dichastopollenites* pollen to Nymphaeaceae (Friis et al., 2001).
Recorded species: (for descriptions see Appendix 1).
Dichastopollenites dunveganensis, Plate II, 14.
Dichastopollenites reticulatus, Plate II, 15–16.
Dichastopollenites sp. 1, Plate II, 17–18.
Dichastopollenites sp. 4 sensu Heimhofer et al. (2007), Plate III, 1–2.

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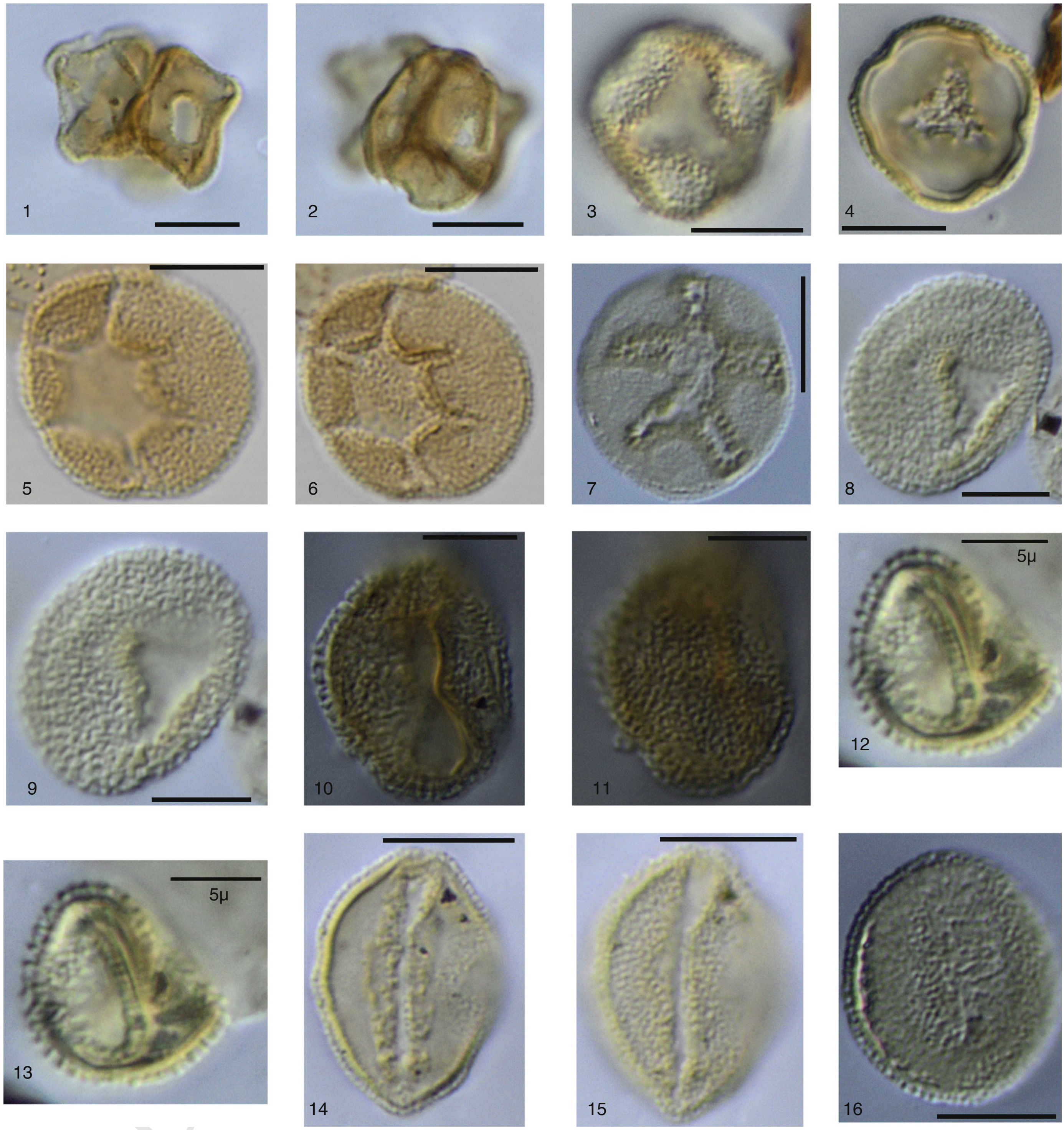

Plate I. Scale bar in all photographs is 10 µm under LM, except otherwise indicated.

1–2.	*Ajatipollis* sp. 1, SJMH-18, 135.8/3.7, 26.2 m
3–4.	*Asteropollis asteroides*, SJMH-2, 143.8/11.9, 7.5 m
5–6.	*Asteropollis* aff. *asteroides*, SSJ-1, 131.4/19.1, 172.4 m
7.	*Asteropollis* sp. 3 sensu Heimhofer et al., 2007, SJMH-78, 125.9/15.3, 83.6 m
8–9.	*Asteropollis* sp. 2 sensu Heimhofer et al., 2007, SJMH-18, 125.8/10.8, 26.2 m
10–11.	*Clavatipollenites* sp. A sensu Doyle and Robbins, 1977, SJMH-4, 130.9/13.7, 10.2 m
12–13.	*Clavatipollenites* sp. 1, SJMH-32, 133.0/8.2, 44 m
14–15.	*Clavatipollenites hughesii*. SJMH-56, 145.0/17.1, 66 m
16.	*Clavatipollenites* sp. 2 sensu Heimhofer et al., 2007, SJMH-11, 128.0/12.4, 17 m

Dichastopollenites sp. 5 sensu Heimhofer et al. (2007), Plate III, 3–4.
Dichastopollenites sp. 6 sensu Heimhofer et al. (2007), Plate III, 5–7.

Genus *Hammenia* Ward 1986

Description and botanical affinity:

Stephanocolpate with 6 brevicolpi, amb circular to sub-circular, pollen grain ~23 μm in diameter. Structure semitectate, columellate; in some forms the columellae are very densely spaced and fused at their heads forming a perforate tectum. The recorded species from São Julião looks similar to *Hammenia* sp. A sensu Burger (1993) and differs from the type species *Hammenia fredericksburgensis* by developing nonequatorial apertures (Burger, 1993).

Recorded species: (for descriptions see Appendix 1).
Hammenia sp. A sensu Burger (1993), Plate III, 8–9.

Genus *Penetetrapites* Hedlund and Norris 1968

Description and botanical affinity:

Tri- or tetra-aperturate pollen grain, with three oval equatorially extended apertures, a fourth aperture developed at one pole. Amb oblate, ~22 μm in diameter. Polar aperture about half the diameter of the three equatorial apertures, almost circular, but variably developed. Sculpture scabrate to faintly perforate.

Recorded species: (for descriptions see Appendix 1).
Penetetrapites mollis, Plate III, 10–11.

Genus *Pennipollis* Friis et al. 2000b

Description and botanical affinity:

Monocolpate, pollen grain with colpus almost reaching the apices, amb circular to sub-circular, 15–27 μm in diameter. Exine acolumellate, sexine detached, reticulate-semitectate; reticulum homobrochate or heterobrochate; lumen diameter 0.5–3.7 μm; muri width 0.5–0.7 μm. Degree of supratectal ornamentation on the muri varies, e.g., verrucae in one row, in two rows or absent. *Pennipollis* sp. 1 looks similar to 'Retimono-knobble' (Penny, 1992). A monocot affinity (Alismatales) of *Pennipollis* has been inferred (Friis et al., 2000b), albeit questioned by Doyle and Endress (2014).

Recorded species: (for descriptions see Appendix 1).
Pennipollis peroreticulatus, Plate III, 12–13.
Pennipollis reticulatus, Plate III, 14–15.
Pennipollis sp. 1, Plate III, 16–17.
Pennipollis sp. 2, Plate III, 18–19.

Genus *Phimopollenites* Dettmann, 1973

Description:

Tricolpoidate pollen grain, amb oblate to sub(circular), ~20 μm in diameter. Structure reticulate-semitectate; reticulum homobrochate;

Plate II. Scale bar in all photographs is 10 μm under LM, except otherwise indicated.

1–2. *Clavatipollenites tenellis*, SJMH-4, 138.8/3.4, 10.2 m
3. *Cretacaeiporites* aff. *polygonalis*, SJMH-178, 126.8/10.4, 160 m
4. *Cretacaeiporites* aff. *scabratus*, SJMH-143, 138.6/7.0, 138.1 m
5–6. *Cretacaeiporites* sp. 1, SJMH-57, 134.4/15.4, 67.3 m
7–9. *Cretacaeiporites* sp. 2, SJMH-52, 133.4/9.9, 59.7 m
10–11. *Cretacaeiporites* sp. 3, SJS-9, 139.0/5.2, 166.4 m
12–13. *Cretacaeiporites* sp. 4, MAG-1, 148.8/7.8
14. *Dichastopollenites dunveganensis*, SJMH-100, 142.1/6.5, 104 m
15. *Dichastopollenites reticulatus*, SJMH-4, 149.6/4.1, 10.2 m
16. *Dichastopollenites reticulatus*, SJMH-4, 149.6/4.1, 10.2 m CLSM image, total stack projection.
17–18. *Dichastopollenites* sp. 1, SJMH-183, 142.3/15.2, 162.2 m

Plate III. Scale bar in all photographs is 10 μm under LM, except otherwise indicated. (see on page 10)

1. *Dichastopollenites* sp. 4 sensu Heimhofer et al., 2007, SJMH-54, 134.8/2.1, 60.7 m
2. *Dichastopollenites* sp. 4 sensu Heimhofer et al., 2007, SJMH-54, 134.8/2.1, 60.7 m, CLSM image, total stack projection.
3–4. *Dichastopollenites* sp. 5 sensu Heimhofer et al., 2007, SJMH-60, 130.7/18.1, 69.6 m
5–6. *Dichastopollenites* sp. 6 sensu Heimhofer et al., 2007, SJMH-119, 131.4/13.7, 170.1 m
7. *Dichastopollenites* sp. 6 sensu Heimhofer et al., 2007, SJMH-119, 131.4/13.7, 170.1 m, CLSM image, total stack projection.
8–9. *Hammenia* sp.A sensu Burger, 1993, MAG-20, 132.5/6.0
10. *Penetetrapites mollis*, SSJ-1, 132.5/20.6, 172.4 m
11. *Penetetrapites mollis*, SSJ-1, 132.5/20.6, 172.4 m, CLSM image, total stack projection.
12–13. *Pennipollis peroreticulatus*, SJMH-101,148.0/14.7, 105.3 m
14–15. *Pennipollis reticulatus*, SJMH-101, 136.6/21.9, 105.3 m
16–17. *Pennipollis* sp. 1, SJMH-12.5, 135.8/7.4, 17.3 m
18. *Pennipollis* sp. 2, SJMH-4, 126.8/7.5, 10.2 m
19. *Pennipollis* sp. 2, SJMH-4, 126.8/7.5, 10.2 m, CLSM image, total stack projection.

Plate IV. Scale bar in all photographs is 10 μm under LM, except otherwise indicated. (see on page 11)

1–2. *Retimonocolpites* sp. 1, SJMH-18, 127.2/18.2 26.2 m
3–4. *Phimopollenites* sp. 1, SJMH-156, 143.3/7.1, 148 m
5–6. *Retimonocolpites dividuus*, SJMH-18, 34.4/17.3, 26.2 m
7–8. *Retimonocolpites* aff. *dividuus*, SJMH-4, 151.0/11.7, 10.2 m
9–10. *Retimonocolpites* sp. 2, SJMH-54, 128.6/17.1, 60.7 m
11–12. *Retimonocolpites* sp. 3, SJMH-21.7124.9/11.5, 31.7 m
13–14. *Retimonocolpites* sp. 4, SJMH-114, 142.1/21.5, 117.4 m
15. *Retimonocolpites* sp. 5 sensu Heimhofer et al., 2007, SJMH-4134.9/8.7, 10.2 m
16–17. *Retimonocolpites* sp. 7, SJMH-178, 140.3/9.7, 160 m
18–20. *Retimonocolpites* sp. 6, SJMH-90, 129.5/14.8, 97.7 m

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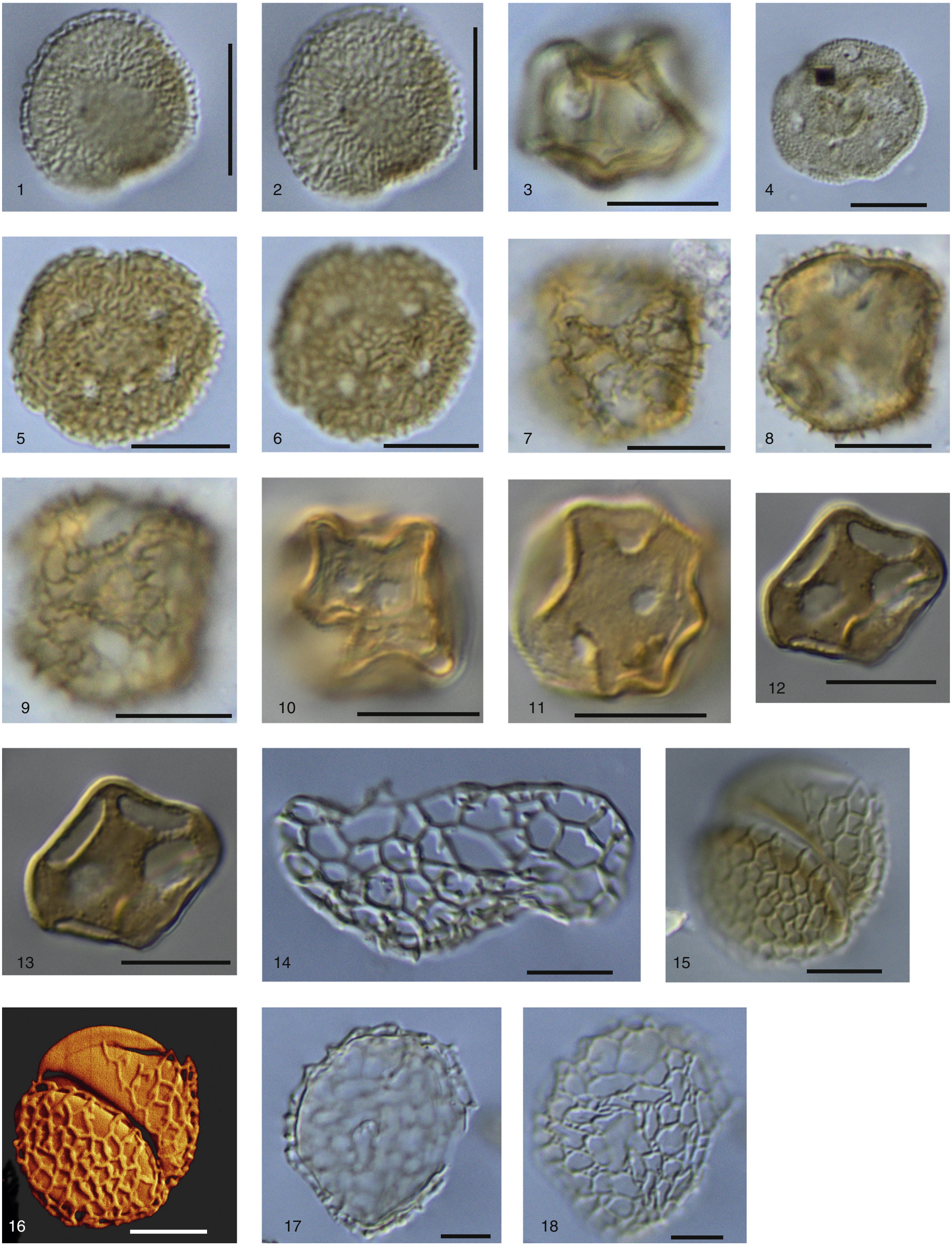
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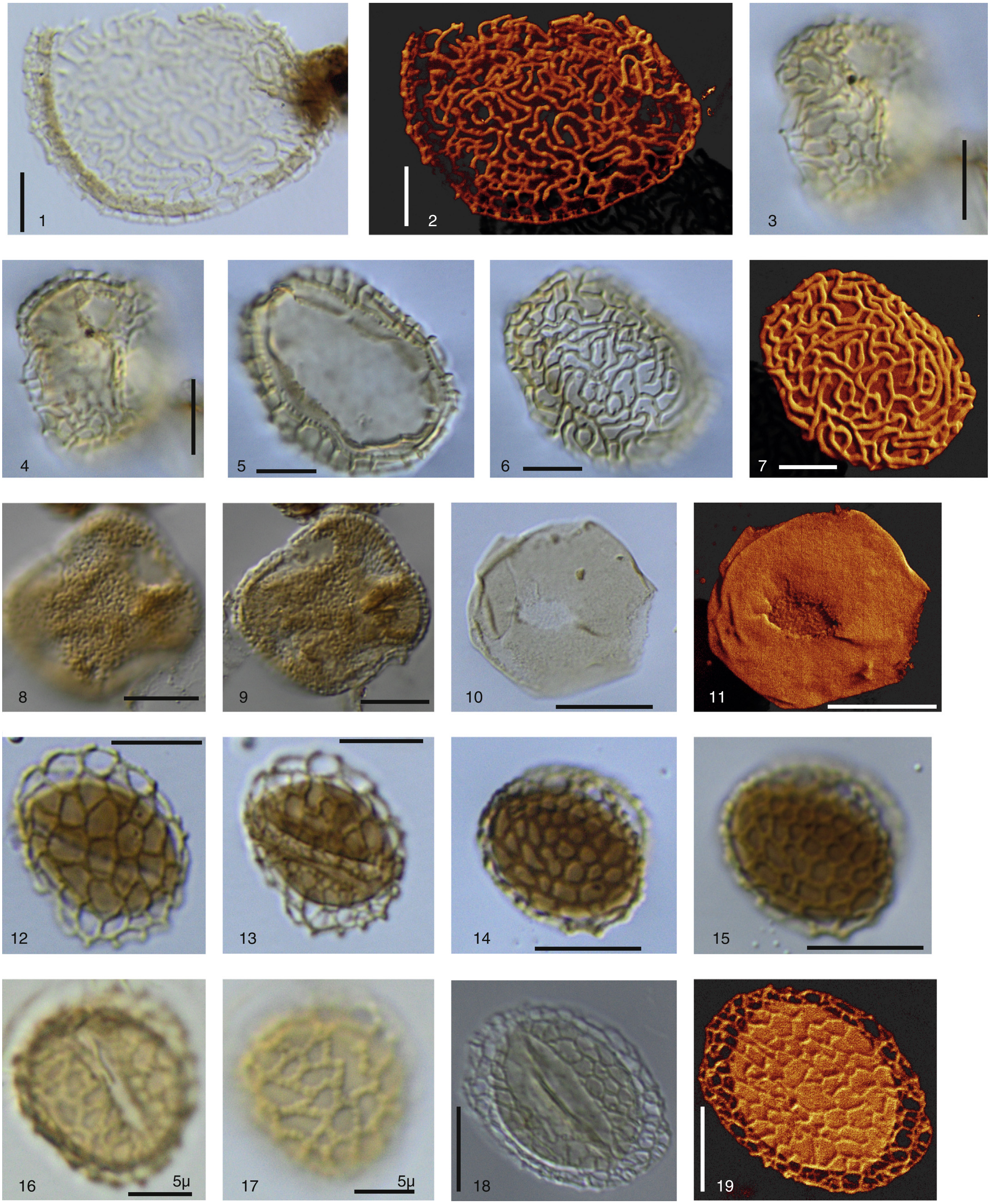

Plate III (*caption on page 8*).

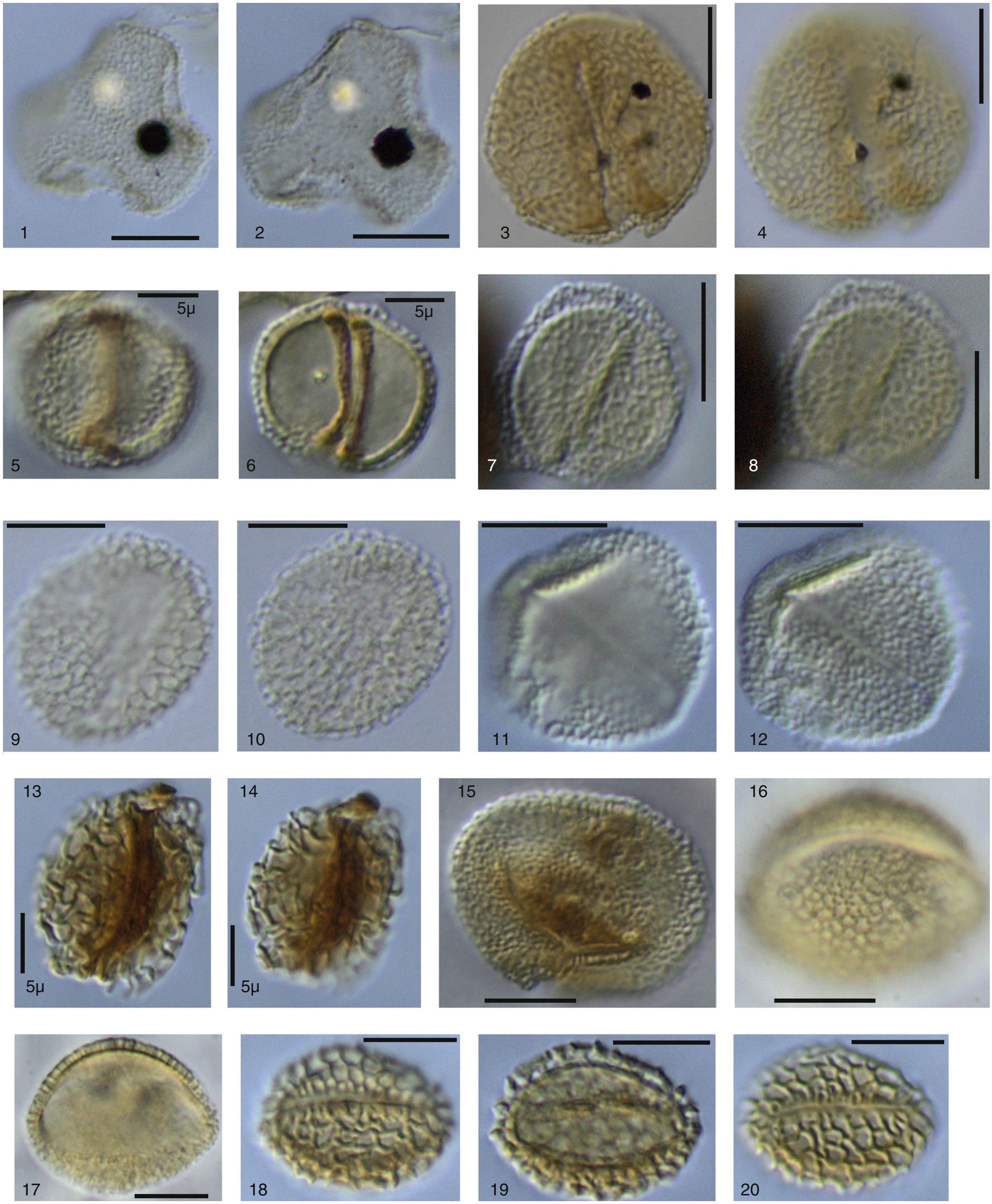

Plate IV (*caption on page 8*).

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lumen diameter 0.8–1.2 μm; muri width 0.4 μm. In the colpal areas the columellae are discrete and interlocked over the colpoids to form operculoid membranes; colpoids elliptically shaped with ragged margins. *Phimopollenites* sp. 1 differs from the type species by its wide aperture.

Recorded species: (for description see Appendix 1).

Phimopollenites sp. 1, Plate IV, 1–2.

Genus *Retimonocolpites* Pierce 1961

Description and botanical affinity:

Monocolpate pollen grain, colpus long, amb elliptical to circular, 15–30 μm in diameter. Structure reticulate-semitectate; reticulum homobrochate or heterobrochate; lumen diameter 0.5–3.6 μm; muri width 0.2–0.6 μm. In some species the muri surface looks verrucate through the overtopping columellae. Following Archangelsky and Archangelsky (2013), forms with both homobrochate and heterobrochate lumen are included in *Retimonocolpites*. *Retimonocolpites* displays a wide range of morphologies in exine structure, muri width, lumen size and shape, hampering a direct comparison to extant pollen groups.

Recorded species: (for descriptions see Appendix 1).

Retimonocolpites dividuus, Plate IV, 3–4.

Retimonocolpites aff. *dividuus*, Plate IV, 5–6. This form differs from *Retimonocolpites dividuus* (Pierce, 1961) by its smaller size (<15 μm).

Retimonocolpites sp. 1, Plate IV, 7–8.

Retimonocolpites sp. 2, Plate IV, 9–10.

Retimonocolpites sp. 3, Plate IV, 11–12.

Retimonocolpites sp. 4, Plate IV, 13–14.

Retimonocolpites sp. 5, Plate IV, 15.

Retimonocolpites sp. 6, Plate IV, 18–20.

Retimonocolpites sp. 7, Plate IV, 16–17.

Genus *Retitrescolpites* Sah, 1967

Description and botanical affinity:

Tricolpate pollen grain, amb circular to sub-circular, 19–23 μm in diameter. Structure reticulate-semitectate; reticulum homobrochate; lumen diameter 1.5–3.0 μm; muri width 0.3–1.1 μm. *Retitrescolpites* is distinguished from *Rousea* by its homobrochate reticulation pattern with large lumen, generally >1 μm, irregular reticulum pattern. The recorded species from São Julião could not be assigned to previously described taxa and are listed as informal species.

Recorded species: (for descriptions see Appendix 1).

Retitrescolpites sp. 1, Plate V, 1–2.

?*Retitrescolpites* sp. 2, Plate V, 3–4.

Retitrescolpites sp. 3, Plate V, 5–6.

?*Retitrescolpites* sp. 4, Plate V, 7–8.

Retitrescolpites sp. 5, Plate V, 9–10.

Retitrescolpites sp. 6, Plate V, 11.

Genus Rousea Srivastava 1969

Description and botanical affinity:

Tricolpate pollen grain, amb circular to sub-circular, 16–26 μm in diameter. Structure reticulate-semitectate; reticulum heterobrochate; lumen diameter 0.3–4.0 μm; muri width 0.3–0.8 μm. In some forms the muri surface looks verrucate through the overtopping columellae. *Rousea* is distinguished from *Retitrescolpites* by its heterobrochate reticulation pattern and from *Tricolpites* by the large lumen size exceeding >1 μm. In this paper, the term 'heterobrochate' lumen applies to the definition of a 'graded reticulum' (large lumen in the equatorial mesocolpium and small lumen near the colpi and at the poles) by Srivastava (1969) and of 'interspersed large and small lumen' by Erdtman (1966). Several *Rousea* species display variations in exine structure, muri width, lumen size and shape not described in previous records and are listed here as informal species. According to Ward (1986), *Rousea* shows similarities to pollen of the Salicaceae.

Recorded species: (for descriptions see Appendix 1).

Rousea georgensis, Plate V, 12–13.

Rousea aff. *prosimilis*, Plate V, 14–15. This form differs from *Rousea prosimilis* (Norris, 1967) by its larger lumen size (0.5–3.0 μm) and thicker muri (0.4–0.7 μm).

Rousea sp. 1, Plate V, 16–17.

?*Rousea* sp. 2, Plate V, 18–19.

Rousea sp. 3, Plate V, 20, Plate VI, 1.

?*Rousea* sp. 4, Plate VI, 2–4.

?*Rousea* sp. 5, Plate VI, 5–6.

?*Rousea* sp. 6, Plate VI, 7–8.

Rousea prosimilis, Plate VI, 9–10.

Rousea sp. 7, Plate VI, 11–12.

Rousea sp. 8, Plate VI, 13–14.

Genus *Senectotetradites* Dettmann 1973

Description and botanical affinity:

Tetrahedral tetrads of tricolpate pollen, colpi narrow, amb single grains prolate to oblate, 22–32 μm in diameter, diameter tetrad 40–44 μm. Structure reticulate-semitectate; reticulum heterobrochate; lumen diameter 1.7–3.0 μm; muri width 0.6 μm.

Recorded species: (for descriptions see Appendix 1).

Senectotetradites varireticulatus, Plate VI, 15–16.

Genus *Stellatopollis* Doyle et al. 1975

Description and botanical affinity:

Monocolpate pollen grain, colpus long, amb elliptical, up to 50 μm long, reticulate-semitectate with muri-bearing supratectal projections with triangular to elliptical heads; often only fragmentary material found. Supratectal elements are arranged in clusters of 4–8 (usually 6) projections. Projections irregularly shaped, mostly oval, round or triangular, apices of triangles directed at centre of lumen. The crotonoid

Plate V. Scale bar in all photographs is 10 μm under LM, except otherwise indicated.

1–2.	*Retitrescolpites* sp. 1, PM-19, 144.0/5.1
3–4.	?*Retitrescolpites* sp. 2, SJMH-57, 147.1/17.9, 67.3 m
5–6.	*Retitrescolpites* sp. 3, SJMH-183, 134.1/8.1, 162.2 m
7–8.	?*Retitrescolpites* sp. 4, SJMH-52, 130.4/2.6, 59.7 m
9–10.	*Retitrescolpites* sp. 5, SJS-16, 137.2/10.1, 170.1 m
11.	*Retitrescolpites* sp. 6, SJMH-36, 149.9/18.2, 47.3 m
12–13.	*Rousea georgensis*, SJMH-18, 133.8/5.6, 26.2 m
14–15.	*Rousea* aff. *prosimilis*, SJMH-24, 149.2/9.5, 35 m
16–17.	*Rousea* sp. 1, SJMH-18, 127.6/4.4, 26.2 m
18–19.	?*Rousea* sp. 2, SJMH-52, 132.0/11.4, 59.7 m
20.	*Rousea* sp. 3, SJMH-147, 129.8/12.2, 139.8 m

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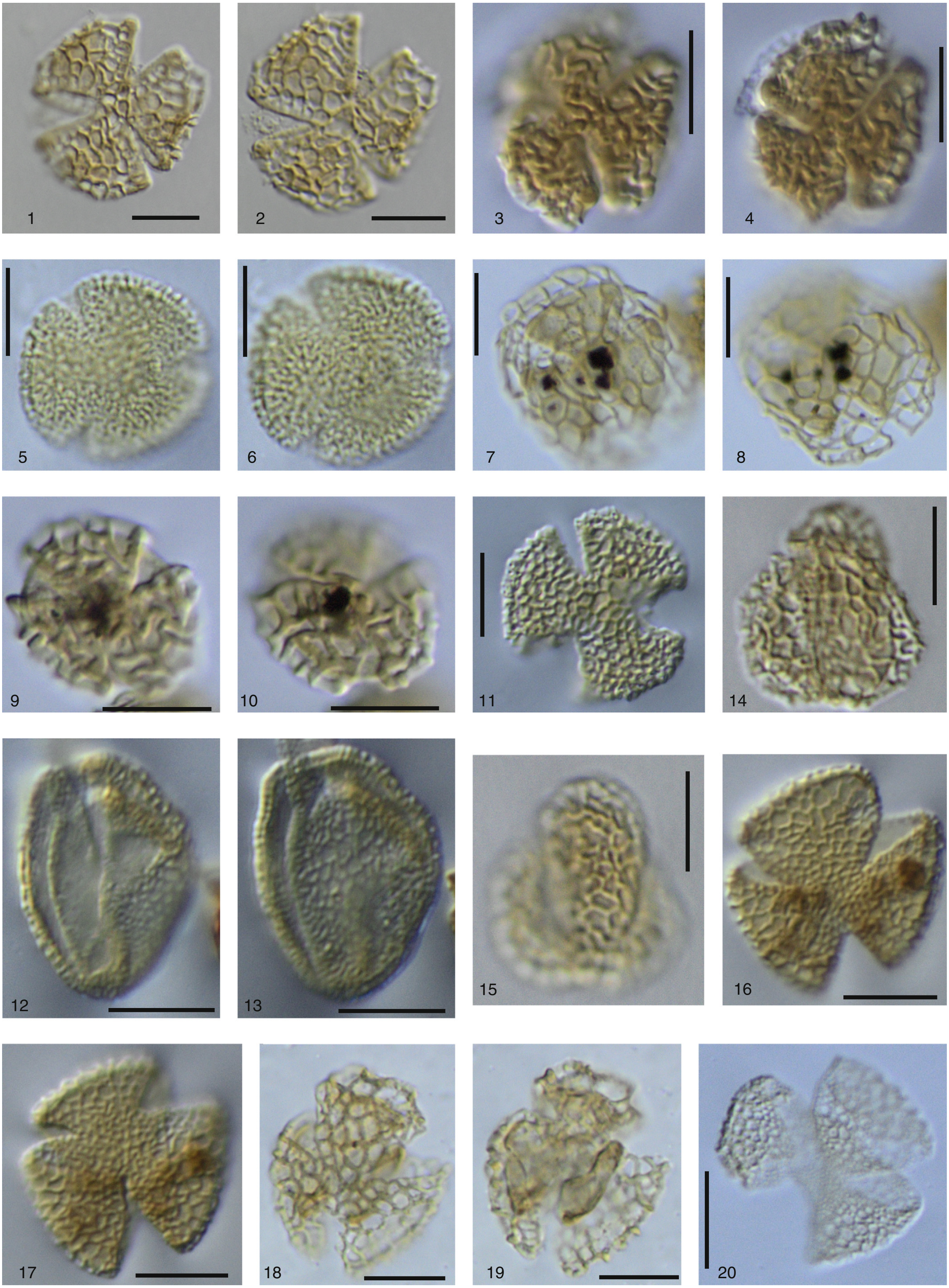

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sculpture and single colpus suggest a possible affinity to pollen of Liliaceae (Doyle et al., 1975).
Recorded species: (for descriptions see Appendix 1).
Stellatopollis barghoornii, Plate VI, 17.
Stellatopollis sp. 1, Plate VI, 18–19.

Genus *Striatopollis* Krutzsch 1959

Description and botanical affinity:

Tricolpate pollen grain, amb circular to sub-circular, 17–28 μm in diameter. Structure striato-reticulate; reticulum homobrochate or heterobrochate; lumen diameter 0.3–2.5 μm, in a number of forms irregular-shaped. In some species the muri surface looks verrucate through the overtopping columellae. Striate tricolpate pollen grains have been found in Albian fossil flowers related to Buxaceae (Pedersen et al., 2007).
Recorded species: (for descriptions see Appendix 1).
Striatopollis paraneus, Plate VI, 20–21.
Striatopollis trochuensis, Plate VI, 22. Plate VII, 1–2.
Striatopollis vermimurus, Plate VII, 3–5.
Striatopollis sp. 1, Plate VII, 6–7.
Striatopollis sp. 2, Plate VII, 8–10.
Striatopollis sp. 3, Plate VII, 11–12.
Striatopollis sp. 4, Plate VII, 13.
Striatopollis sp. 5, Plate VII, 14–15.
Striatopollis sp. 6, Plate VII, 16–18.

Tetracolpate form

Tetracolpate pollen grain, colpi long and broadly opened, circular to sub-circular, 17 μm in diameter. Structure reticulate-semitectate; reticulum homobrochate; lumen diameter 0.5–0.8 μm; muri width 0.6 μm.
Recorded species: (for descriptions see Appendix 1).
Tetracolpate form 1, Plate VII, 19–20.

Genus *Tricolpites* Cookson ex. Couper 1953

Description and botanical affinity:

Tricolpate pollen grain, amb circular to sub-circular, 12–32 μm in diameter. Structure reticulate-semitectate; reticulum homobrochate or heterobrochate; lumen diameter 0.2–0.9 μm; muri width 0.2–0.6 μm. In some species the columellae are very densely spaced and fused at their heads forming a perforate tectum. *Tricolpites* is distinguished from *Retitrescolpites* and *Rousea* by the small lumen <1 μm.
Recorded species: (for descriptions see Appendix 1).
Tricolpites aff. *albiensis*, Plate VIII, 1–2. This form differs from *Tricolpites albiensis* (Kemp, 1968) by its larger lumen size (0.4–0.7 μm).
Tricolpites blechrus, Plate VIII, 3–4.
Tricolpites crassimurus, Plate VIII, 5–7.
Tricolpites aff. *fragosus*, Plate VIII, 8–10. This form differs from *Tricolpites fragosus* (Hedlund and Norris, 1968) by its larger size (18–26 μm).
Tricolpites sagax, Plate VIII, 11.
Tricolpites vulgaris, Plate VIII, 12–14.
Tricolpites sp. 1, Plate VIII, 15–16.

Tricolporate forms

Description and botanical affinity:

Tricolporate pollen grain, amb circular to oblate, ~20 μm in diameter. Structure striate, columellate, semitectate or reticulate-semitectate; muri width 0.3–0.4 μm. In some forms the columellae are very densely spaced and fused at their heads forming a perforate tectum.
Recorded species: (for descriptions see Appendix 1).
Tricolporate form 1, Plate VIII, 17–18.
Tricolporate form 2, Plate VIII, 19–20.
Tricolporate form 3, Plate VIII, 21–22.

4.2. Stratigraphic distribution of angiosperm pollen

Relative abundances of the angiosperm pollen vary between 1 and 20%, but rarely exceed 10% of the total spore–pollen count (Fig. 3). The accompanying palynoflora is dominated by non-saccate gymnosperm pollen such as *Classopollis* and *Inaperturopollenites*, whereas *Araucariacites*, *Callialasporites*, *Exesipollenites*, *Cycadopites* and several spore types (e.g., *Cicatricosisporites*, *Leptolepidites*, *Deltoidospora*) occur only in subordinate numbers. Bisaccate pollen (average 1.4%) are consistently present but in low numbers.

Plate VI. Scale bar in all photographs is 10 μm under LM, except otherwise indicated.

1.	*Rousea* sp. 3, SJMH-147, 129.8/12.2, 139.8 m
2–3.	?*Rousea* sp. 4; SJMH-21.7, 127.1/14.1, 31.7 m
4.	*Rousea* sp. 4; SJMH-21.7, 127.1/14.1, 31.7 m, CLSM image, total stack projection.
5–6.	?*Rousea* sp. 5, SSJ-1, 141.7/6.0, 172.4 m
7–8.	?Rousea sp. 6, MAG-33, 137.7/21.4
9–10.	*Rousea prosimilis*, SJS-16, 132.3/3.0, 170.1 m
11–12.	*Rousea*, sp. 7, SSJ-1, 133.7/3.8, 172.4 m
13–14.	*Rousea* sp. 8, SJMH-178, 129.8/9.5, 160 m
15–16.	*Senectotetradites varireticulatus*, SJMH-57, 139.1/18.8, 67.3 m
17.	*Stellatopollis barghoornii*, SJMH-114, 135.1/16.9, 117.4 m
18–19.	*Stellatopollis* sp. 1, SJS-16, 146.5/14.1, 170.1 m
20–21.	*Striatopollis paraneus*, SJMH-119, 147.0/8.0, 121.8 m
22.	*Striatopollis trochuensis*, SSJ-1, 130.0/11.3, 172.4 m, CLSM image, total stack projection.

Plate VII. Scale bar in all photographs is 10 μm under LM, except otherwise indicated. (see on page 16)

1–2.	*Striatopollis trochuensis*, SSJ-1, 130.0/11.3, 172.4 m
3–5.	*Striatopollis vermimurus*, SJMH-54, 145.4/4.9, 60.7 m
6–7.	*Striatopollis* sp. 1, SJMH-21.7, 148.6/20.4, 31.7 m
8.	*Striatopollis* sp. 2, MAG-10, 149.6/21.4, CLSM image, total stack projection.
9–10.	*Striatopollis* sp. 2, MAG-10, 149.6/21.4
11–12.	*Striatopollis* sp. 3, SJMH-85, 141.8/7.3, 92.6 m
13.	*Striatopollis* sp. 4, SJMH-90, 137.0/7.0, 97.7 m
14–15.	*Striatopollis* sp. 5, SJMH-57, 145.3/12.2, 67.3 m
16–18.	*Striatopollis* sp. 6, SJMH-78, 128.8/7.2, 83.6 m
19–20.	Tetracolpate form sp. 1, SJMH-88, 137.3/16.5, 95.85 m

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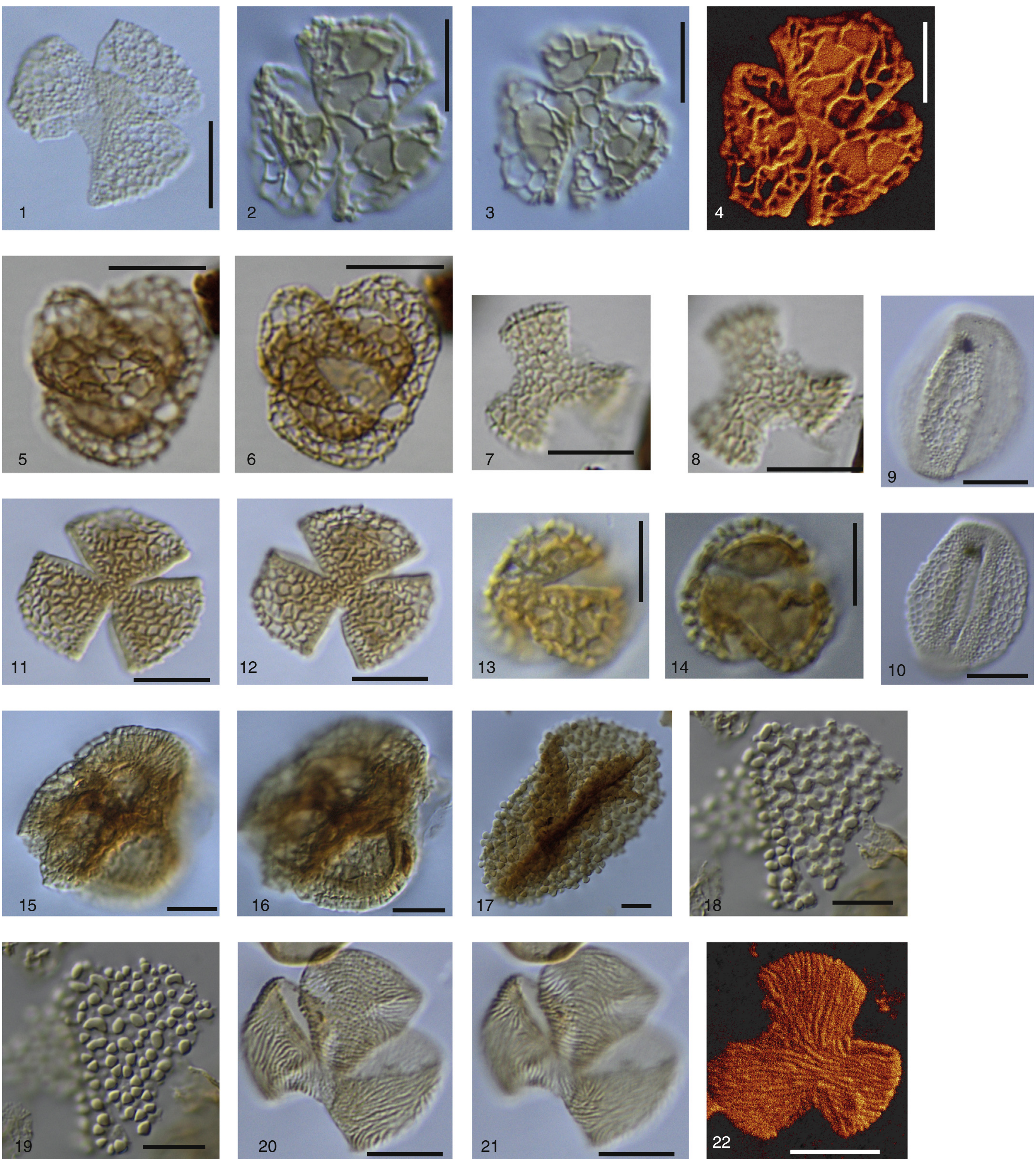
4.2.1. Early Albian (0 to 18 m)

In the early Albian (represented by 5 samples) angiosperm pollen abundances fluctuate between 2 and 7% (average 5.3%) of the total palynoflora. The assemblages are characterized by monocolpate grains (17 species) belonging to *Asteropollis asteroides*, *Clavatipollenites hughesii*, *Clavatipollenites tenellis*, *Dichastopollenites reticulatus*, *Dichastopollenites dunveganensis*, *Pennipollis peroreticulatus*, *Pennipollis reticulatus*, and *Retimonocolpites dividuus*, as well as several informal species (Fig. 3). Rare occurrences of tricolpate and polyporate pollen grains are also found and include *Striatopollis vermimurus*, *Ajatipollis* sp. 1 and



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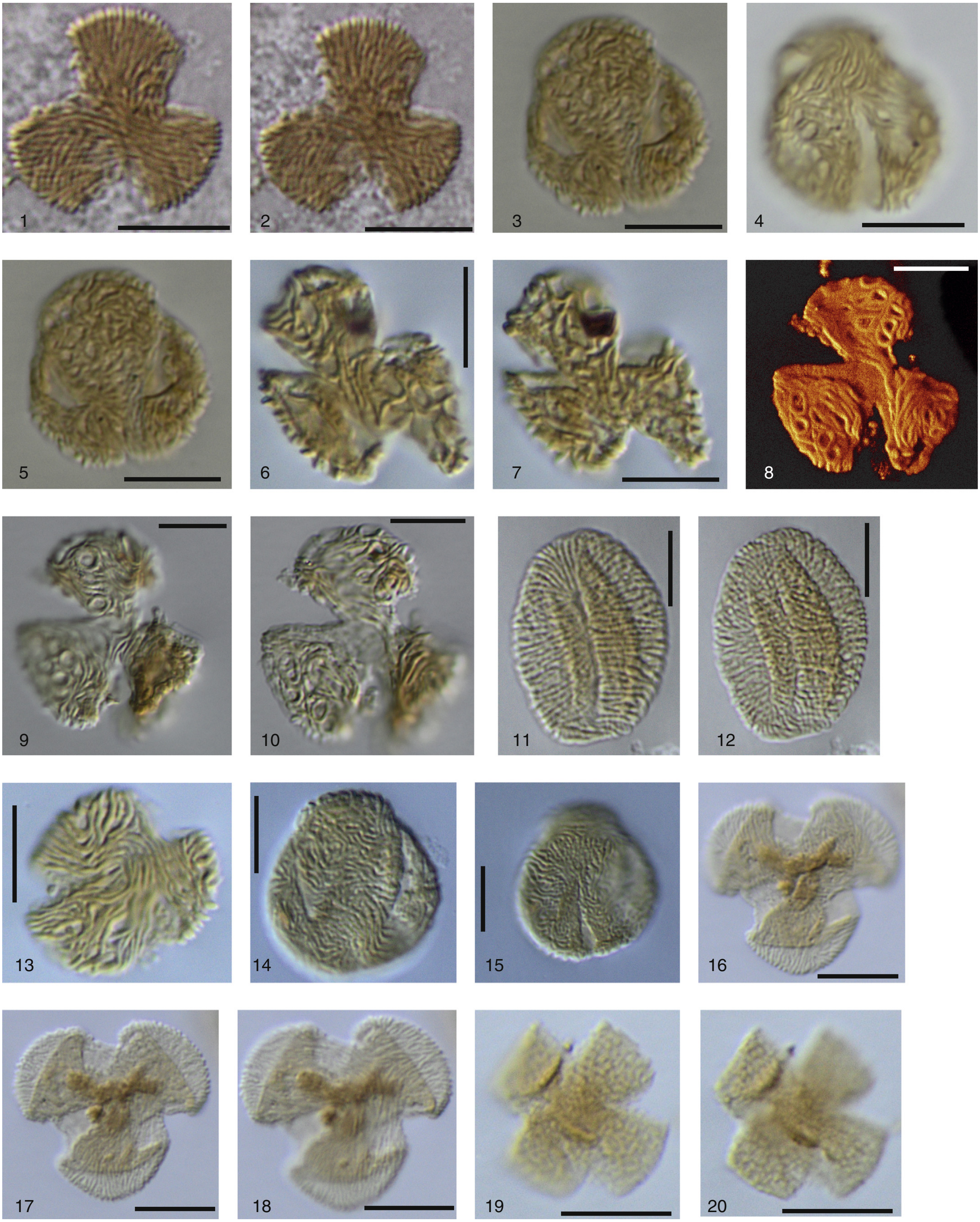

Plate VII (*caption on page 14*).

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Cretacaeiporites sp. 4 at 10 m. *Tricolpites* aff. *fragosus*, *Tricolpites sagax* and *Striatopollis paraneus* first appear at 17 m.

4.2.2. Middle Albian (18 to 44 m)

During the middle Albian (represented by 7 samples) the relative abundance of angiosperm pollen is slightly higher and varies between 2 and 12% (average 6.9%). Newly appearing monocolpate pollen include members of the genera *Stellatopollis*, *Asteropollis* and *Clavatipollenites*. *Dichastopollenites* sp. 4 sensu Heimhofer et al. (2007) and *D*. sp. 6 sensu Heimhofer et al. (2007) first appear at 31 m. First occurring tricolpate genera include *Rousea*, *Phimopollenites* and *Striatopollis trochuensis* at 25 m, *Tricolpites vulgaris* at 25 m, *Rousea georgensis* at 26 m, *Rousea* aff. *prosimilis* at 31 m and *Retitrescolpites* sp. 1 at 35 m (Fig. 3).

4.2.3. Late Albian to early Cenomanian (44 to 175 m)

During the late Albian to early Cenomanian (represented by 56 productive samples) the angiosperm pollen abundance fluctuates between 1 and 20% (average 8%). A single sample records a high relative angiosperm abundance of 39% strongly dominated by *Pennipollis*. These high values are most probably an artefact, related to the presence of a pollen-sac in the processed sample. A distinct rise in angiosperm pollen abundance is observed between 85 and 110 m, followed by a subsequent decline towards background values of less than 10%. The late Albian shows a striking increase in tri- and poly-aperturate pollen within this interval.

Among monocolpate pollen forms, several (total of 7) informal species of the *Retimonocolpites*, *Asteropollis* and *Dichastopollenites* groups appear for the first time during the late Albian; *Dichastopollenites* sp. 5 sensu Heimhofer et al. (2007) first appears at 61 m. Newly appearing tricolpate pollen taxa are represented by *Striatopollis* (three new informal species), *Rousea* (seven new informal species) and *Retitrescolpites* (four new informal species). The diversification among *Tricolpites* pollen is indicated by the FO of *Tricolpites* aff. *albiensis* (at 67 m), *Tricolpites crassimurus* (at 84 m) and *Tricolpites blechrus* (at 138 m). Polyporate pollen grains with a FO in the late Albian include rare occurrences of *Cretacaeiporites* sp. 2 (at 60 m), *Cretacaeiporites* sp. 1 (at 67 m) and *Cretacaeiporites* aff. *polygonalis* (at 145 m). *Cretacaeiporites* sp. 3 and *Cretacaeiporites* aff. *scabratus* first appear during the latest Albian. Rare occurrences of tricolporate pollen in the late Albian are evidenced by the FO of Tricolporate form 1 (at 84 m), Tricolporate form 2 (at 90 m) and Tricolporate form 3 (at 160 m). The obligate tetrad of *Senectotetradites varireticulatus* appears for the first time at 67 m, and *Penetetrapites mollis* at 122 m. Important last occurrences (LO) include *Striatopollis vermimurus* (at 122 m), *Retimonocolpites dividuus* (at 131 m), *Dichastopollenites* sp. 4 sensu Heimhofer et al. (2007) (at 145 m), *D*. sp. 5 sensu Heimhofer et al. (2007) (at 151 m) and *D*. sp. 6 sensu Heimhofer et al. (2007) (at 153 m).

5. Discussion

5.1. Timing of angiosperm pollen evolution and biostratigraphic significance

The Cresmina section represents another important archive to track angiosperm pollen distributions during the Albian in the Lusitanian Basin. Located about 20 km to the south of São Julião, the section covers 129 m of early to late Albian deposits with diverse angiosperm pollen assemblages. The angiosperm pollen distribution in these near-shore deposits has been extensively studied (Hasenboehler, 1981; Chapman, 1982; Heimhofer et al., 2007, 2012). Recently the two sections have been correlated and calibrated using strontium and carbon-isotope stratigraphy, as well as dinoflagellate cyst biostratigraphy and age-diagnostic ammonites and rudists (Horikx et al., 2014). The Cresmina section covers an extended early Albian succession, whereas the late Albian strata are more carbonate rich and reduced in thickness (~30 m). The São Julião section with an extended late Albian sequence is covered by 56 samples (compared to three samples from the Cresmina record) and therefore significantly expands the angiosperm pollen record towards the early Cenomanian in the Lusitanian Basin. Despite the absence of some angiosperm pollen types in the São Julião section as compared to the Cresmina section (e.g., *Artiopollis praecox* and *Racemonocolpites exoticus*), both sections show very similar assemblages in the stratigraphically overlapping part (sensu Heimhofer et al., 2007, Appendix 1). Whereas the angiosperm record of monocolpate pollen is similar in the two sections, a significantly higher diversity of tricolpate pollen is recorded from São Julião. This clear discrepancy and underrepresentation of tricolpate pollen in the Cresmina record may be related to differences in the composition of the vegetation thriving in the corresponding catchment area in the hinterland of the two sections.

The angiosperm pollen assemblage at São Julião section was previously studied by Médus and Berthou (1980). According to these authors, the lower part of the São Julião section, named 'Foz do Folcao', was characterized by a high diversity of tricolpate, tricolporoidate and tricolporate pollen, and a mid- to late Albian age was attributed to it. Unfortunately, a more detailed comparison with this record is hampered by the low stratigraphic resolution of the data-set (11 productive samples), the unclear stratigraphic position of the palynological samples and the scant documentation.

The São Julião section provides valuable biostratigraphic information on the first appearance of the various morphological groups and important taxa of angiosperm pollen (Fig. 4). The early Albian angiosperm pollen assemblages are dominated by monocolpate pollen groups (*Asteropollis*, *Clavatipollenites*, and *Pennipollis*). Most of these groups have been recorded in pre-Albian strata of the Lusitanian Basin and are long-ranging (Heimhofer et al., 2007). *Asteropollis asteroides* is known to appear first during the Barremian–Aptian and to range up to the Cenomanian (Zhang et al., 2014), whereas *Clavatipollenites* is known from the Valanginian (Gübeli et al., 1984;

Plate VIII. Scale bar in all photographs is 10 μm under LM, except otherwise indicated.

1–2.	*Tricolpites* aff. *albiensis*, SJMH-78, 136.5/19.5, 83.6 m
3–4.	*Tricolpites blechrus*, SJMH-143, 127.9/20.5, 138.1 m
5–7.	*Tricolpites crassimurus*, SJMH-78, 148.0/15.4, 83.6 m
8–10.	*Tricolpites* aff. *fragosus*, SJMH-11, 135.5/5.9, 17 m
11.	*Tricolpites sagax*, SJMH-18, 139.6/21.4, 26.2 m
12–14.	*Tricolpites vulgaris*, SJMH-128, 137.3/17.5, 126 m
15–16.	*Tricolpites* sp. 1, SJMH-119, 129.1/11.0, 121.8 m
17–18.	Tricolporate form 1, SJMH-78, 150.2/9.0 83.6 m
19–20.	Tricolporate form 2, SJMH-143, 140.5/8.0, 138.1 m
21–22.	Tricolporate form 3, SJMH-178, 139.3/16.0, 160 m
23–24.	Triporate form 1, SJMH-177, 143.2/10.1, 158.9 m

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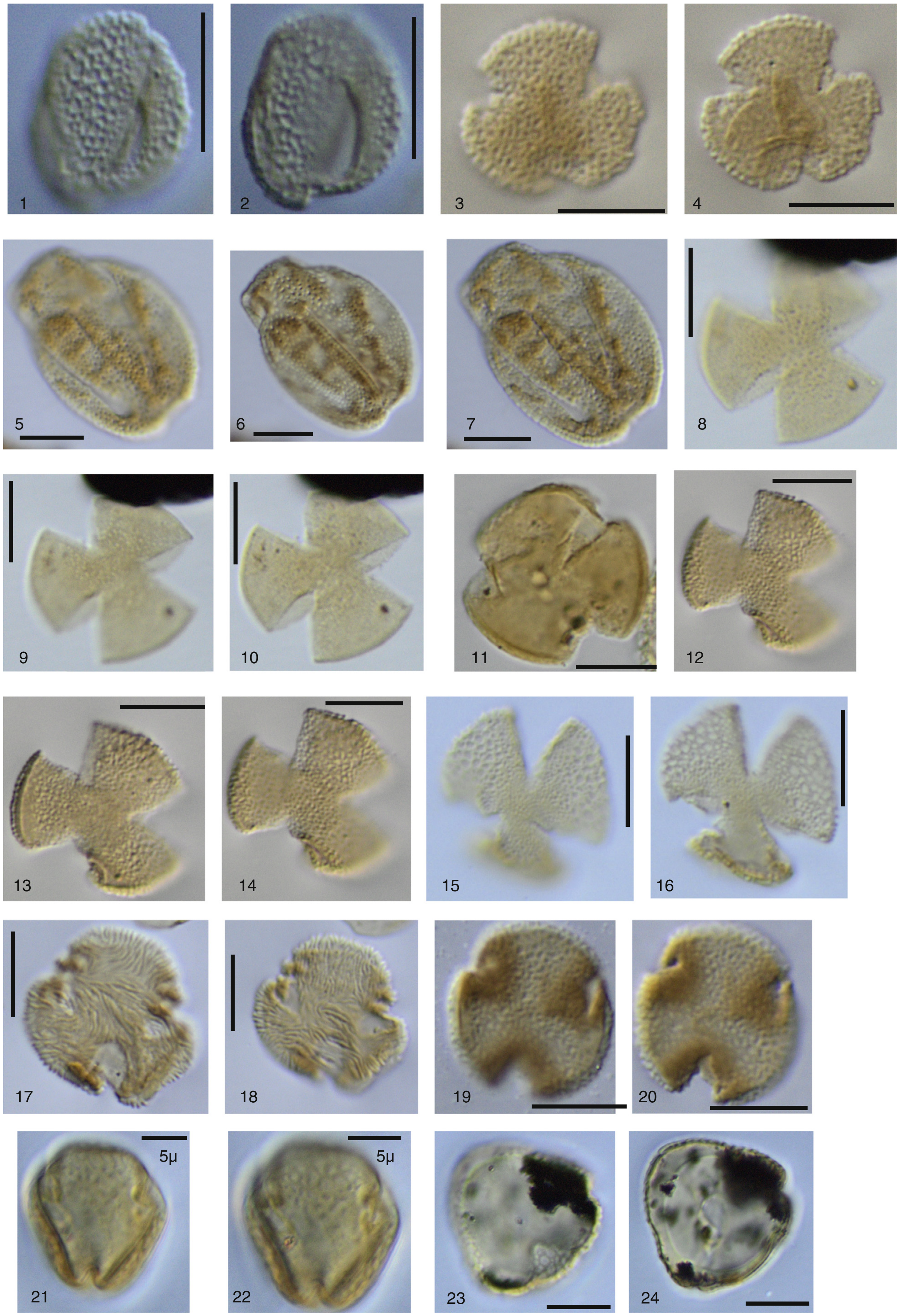
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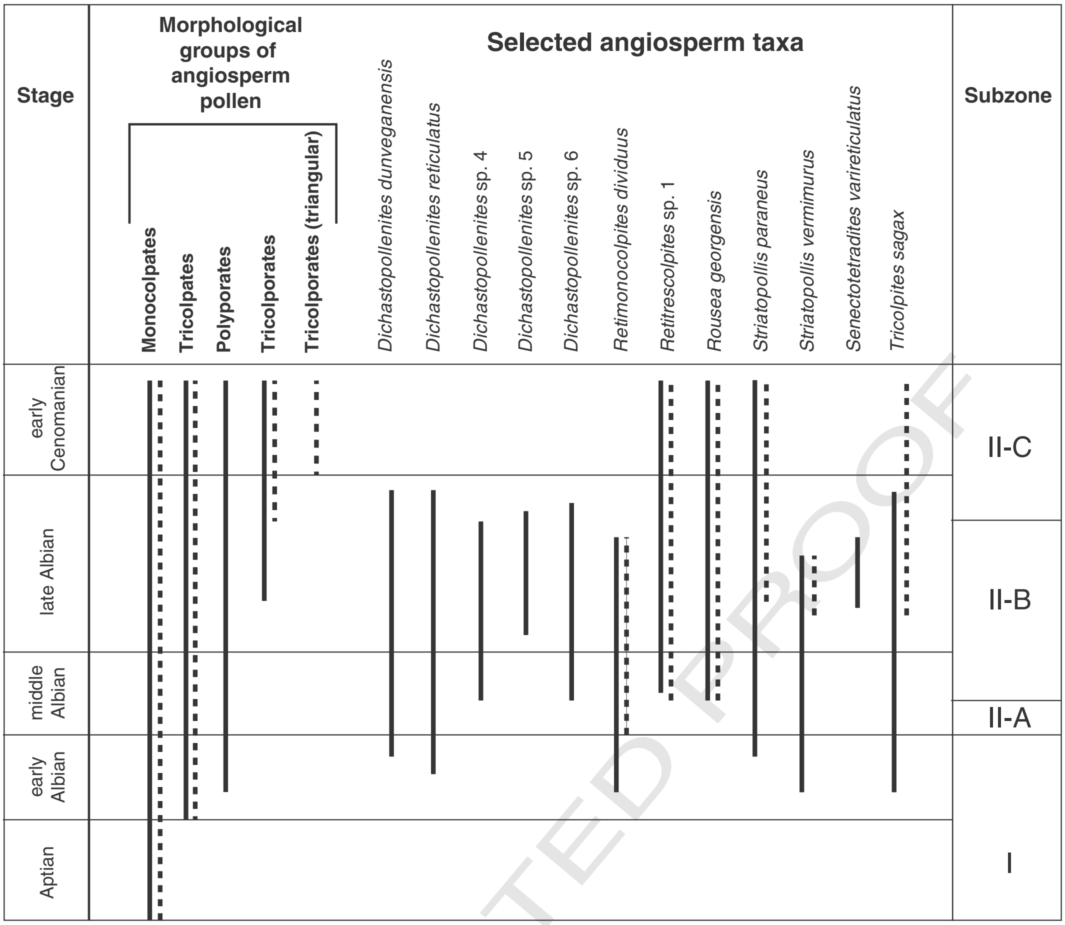

Fig. 4. Biostratigraphic age-range of selected angiosperm pollen taxa and morphological groups from the São Julião section and stratigraphic correlation to the palynological Subzones of the Potomac Group succession, eastern USA. Solid lines represent angiosperm pollen range chart from the São Julião section; dashed lines show the angiosperm pollen data from the Potomac Group succession.

Hughes and McDougall, 1987; Hughes, 1994). *Pennipollis* (as *Peromonolites*, Brenner, 1963) is known from the Aptian up to the Cenomanian (Doyle and Robbins, 1977; Doyle, 1992; Heimhofer et al., 2007; Archangelsky et al., 2009). *Retimonocolpites dividuus* was first reported in North America from the Albian (e.g., Singh, 1971; Doyle and Robbins, 1977; Ward, 1986) and from strata of early Albian age in England (as *Clavatipollenites rotundus*, Kemp, 1968). *Retimonocolpites dividuus* ranges from the early Albian to the late Albian in São Julião and Cresmina (Heimhofer et al., 2007; Fig. 4) and to the Cenomanian in North America (Hedlund and Norris, 1968; Doyle and Robbins, 1977).

The FO of *Cretacaeiporites* sp. 4 in the early Albian represents one of the earliest records of polyporate pollen at mid-latitudes (Fig. 4). Polyporate pollen grains have been recorded by Hasenboehler (1981), Chapman (1982) and Barrón et al. (2015) from the late Albian of the Lusitanian Basin and from Spain. Jardiné and Magloire (1965), Herngreen (1973), Ibrahim (2002) and El Beialy et al. (2011) reported *Cretacaeiporites* in Albian strata from low palaeolatitudes in Africa and South America. The presence of *Cretacaeiporites* at São Julião represents a tropical floral element from lower latitudes and supports the concept that Iberia was located in a transitional area between the Northern Gondwana and Southern Laurasia floral zones.

Tricolpites and *Striatopollis* represent the first tricolpate pollen in the São Julião record (Fig. 3). The presence of *Tricolpites sagax*, *Striatopollis paraneus*, and *Striatopollis vermimurus* in early Albian strata predates earlier findings of these species at mid-latitudes. *Tricolpites sagax* was previously described from the middle Albian to early Cenomanian in North America and Spain (Norris, 1967; Ward, 1986; Barrón et al., 2015). At lower latitudes, *Striatopollis* is reported from the Barremian–Aptian in Egypt, Gabon and Congo and represents one of the oldest tricolpate pollen group (Doyle et al., 1977; Penny, 1988). At mid-latitudes *S. paraneus* and *S. vermimurus* were found in middle Albian to early Cenomanian strata from Canada, USA and Iberia (Norris, 1967; Hasenboehler, 1981; Ward, 1986; Villanueva-Amadoz et al., 2011). At São Julião *S. paraneus* continues from the early Albian onwards into the Cenomanian, whereas *S. vermimurus* disappears in the latest Albian (Fig. 4). The presence of *Striatopollis trochuensis* at São Julião (middle to late Albian) slightly postdates the finding of Heimhofer et al. (2007) from early Albian strata in Portugal. Other findings of *S. trochuensis* include from the late Albian in Spain (Barrón et al., 2015) and North America (Norris, 1967; Ward, 1986) and the Cenomanian in Egypt (Ibrahim, 1996, 2002).

Noteworthy are the FOs of several species of *Dichastopollenites* (*D.* sp. 4 sensu Heimhofer et al., 2007, *D.* sp. 5 sensu Heimhofer et al., 2007 and *D.* sp. 6 sensu Heimhofer et al., 2007) during the middle and late Albian (Figs. 3, 4). In the Lusitanian Basin these conspicuous pollen are relatively common in the palynological assemblages of middle to late Albian age (see also Heimhofer et al., 2007). *Dichastopollenites* sp. 5 first appears in the lower part of the late Albian (Heimhofer et al., 2007), whereas *D.* sp. 4 and *D.* sp. 6 first appear during the middle Albian (Fig. 4). The presence of *Dichastopollenites dunveganensis* in the early Albian coincides with the Cresmina record (Heimhofer et al., 2007), whereas the early Albian FO of *Dichastopollenites*

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reticulatus significantly extends the stratigraphic age range of this species (Fig. 4). Previously, *D. reticulatus* was known only from the Cenomanian in Canada (May, 1975).

At São Julião two species (*Penetetrapites mollis* and the obligate tetrads *Senectotetradites varireticulatus*) occur from the late Albian onwards (Fig. 4). *Penetetrapites mollis* has a global distribution and is a common element in palynological assemblages from the middle Albian to the Cenomanian (Hedlund and Norris, 1968; Ward, 1986; Villanueva-Amadoz et al., 2011), whereas *S. varireticulatus* is documented from the latest Albian onwards from Spain and Australia (Burger, 1993; Villanueva-Amadoz et al., 2011; Sender et al., 2012; Barrón et al., 2015).

The FO of tricolporate pollen grains in the lower part of the late Albian highlights a new step in angiosperm pollen evolution (Fig. 4) and corroborates the first appearance of tricolporates in previous studies. Tricolporate pollen have been reported from the late Albian in the Lusitanian Basin (Hasenboehler, 1981; Chapman, 1982), as well as from Canada, Egypt and Spain (Singh, 1983; El-Beialy et al., 2010; Sender et al., 2012; Barrón et al., 2015).

5.2. Comments on the age of the Potomac succession

The Potomac Group succession is characterized by the relatively low diversity of monocolpate angiosperm pollen and the absence of *Dichastopollenites* and polyporate pollen grains, but conversely it has a continuous and consistent presence of several tricolpates and monocolpates with a graded reticulum of the *Liliacidites* type compared to the Albian pollen records from shallow marine records in Portugal (Doyle and Robbins, 1977; Heimhofer et al., 2007). However, these continental deposits lack independent age control and contain a number of major discontinuities. Previously, the dating of the palynological zones (Zone I and Subzone II-A) in the Potomac Group succession was revised based on comparison with stratigraphically well-constrained angiosperm pollen records from Cresmina and Luz in the Lusitanian Basin by Hochuli et al. (2006). The São Julião record expands the Portuguese pollen record into the early Cenomanian and allows a direct comparison with Subzones II-B and II-C of the Potomac succession. According to Doyle and Hickey (1976) and Doyle and Robbins (1977), the angiosperm pollen composition in the middle part of Subzone II-B is very similar to the palynological assemblages of middle Albian marine strata in Oklahoma, whereas the upper part of Subzone II-B is dated as late Albian (Hedlund and Norris, 1968, 1986). In contrast, Hochuli et al. (2006, p. 591) suggested a late Albian age for the entire Subzone II-B based on the presence of the late Albian index species *Cupuliferoidaepollenites parvulus*.

The lower part of Subzone II-B of the Potomac Group is marked by the FO of tricolpate pollen types and several of these (e.g., *Tricolpites* aff. *albiensis*, *Tricolpites crassimurus*) also occur at São Julião. However, the FOs and stratigraphic ranges of these species vary compared to São Julião and hamper a clear age assignment to the lower part of Subzone II-B. A typical element of Subzone II-B is *Tricolpites* sp. B sensu Doyle and Robbins (1977) that looks very similar to *Retitrescolpites* sp. 1 (Plate V, 1–2, Appendix 1). *Retitrescolpites* sp. 1 first appears in the middle Albian (Fig. 4) and *Rousea georgensis*, another Subzone II-B marker, appears within the middle Albian at São Julião (Fig. 4). Based on the appearance of *Retitrescolpites* sp. 1 and *R. georgensis* in the lower part of Subzone II-B, this level could be tentatively placed in the middle to earliest late Albian.

As shown in the range chart compiled by Hochuli et al. (2006) from the data of Doyle and Robbins (1977), the transition from the lower to the upper part of Subzone II-B is characterized by a ‘sudden’ diversity increase, suggesting another possible hiatus. This interval shows a further diversification of several tricolpate pollen grains with long stratigraphic ranges. Of special interest, however, is the striking LO of *Striatopollis vermimurus* in this interval and its disappearance from the palynological record during the latest Albian at São Julião (Doyle and Robbins, 1977; Hochuli et al., 2006; Fig. 4). Therefore, the LO of *S. vermimurus* in the upper part of Subzone II-B is interpreted to represent a stratigraphic marker for a latest Albian age.

According to Doyle and Robbins (1977), Subzone II-B can be separated from the lower Subzone II-C by the presence of small, psilate tricolporates. Tricolporates are rare and hard to recognize and as these authors already indicate, “it is easy to confuse Subzone II-C floras with depauperate Subzone II-B floras” (Doyle and Robbins, 1977, p. 58). A late Albian age for the lower part of Subzone II-C is corroborated by the FO of several tricolporates in the late Albian at São Julião (Figs. 3, 4). The FO of tricolporate pollen grains with a conspicuous triangular shape (*Tricolporoidites triangulus*) in Subzone II-C marks an important event in angiosperm pollen morphology evolution. Furthermore, tricolporates become increasingly more abundant and diverse in younger (Zone III) sediments of the Potomac Group succession. Despite the presence of several tricolporate pollen in the late Albian in the Portuguese sections (Figs. 3, 4) triangular-shaped tricolporate pollen grains have not been recorded. The absence of such forms in the São Julião record may therefore point to an early Cenomanian age for the upper part of Subzone II-C.

6. Conclusions

(1) The São Julião section shows the distribution of new and previously documented angiosperm pollen types considered typical for the mid-latitudes. The angiosperm pollen record documents rich assemblages of monocolpate pollen (30 taxa) of monocot or “magnoliid” affinity and 49 taxa of tri- and poly-aperturate pollen of eudicot affinity.
(2) The early Albian angiosperm pollen record is characterized by the common occurrence of monocolpate pollen grains and rare but diverse tricolpate grains. A striking diversification phase of tricolpates is observed during the middle and late Albian, whereas the FOs of several polyporate pollen species in the early Albian and FOs of tricolporate pollen in the late Albian highlight important events in angiosperm pollen evolution.
(3) Despite the conspicuous increase in diversity, relative angiosperm pollen abundances remain low throughout most of the Albian with an average of $<10\%$ of the total palynoflora.
(4) A direct correlation of the São Julião record with the Potomac Group succession in the eastern USA suggests a middle-late Albian age for the lower part of Subzone II-B and a late Albian age for the upper part of Subzone II-B and lower Subzone II-C. Triangular-shaped tricolporate pollen are absent in the late Albian at São Julião record. The presence of these pollen types in the upper part of Subzone II-C points to an age not older than early Cenomanian.

Uncited references

Couper, 1958
Dettmann, 1973
Krutzsch, 1959
Phillips and Felix, 1972
Sah, 1967
Srivastava, 1967
Srivastava, 1977
Ward, 1983

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Appendix 1

Genus *Ajatipollis* Krutzsch 1970

Species	Author	Size (µm)	Amb/ Shape	Exine (µm)	Sexine (µm)	Nexine (µm)	Reticulum	Columellae (µm)	Aperture Type	Plate
Ajatipollis sp. 1	Informal species	21-25 (tetrad) 10-13 (grain)	permanent tetrad	columellate, semitectate 2.2	1.4-1.7	0.5	perforate	densely spaced head Ø 0.4µ	Triporate pore size 5-6 µm	Plate I, Fig. 1-2

Genus *Asteropollis* Hedlund and Norris 1968

Species	Author	Size (µm)	Amb/ Shape	Exine (µm)	Sexine (µm)	Nexine (µm)	Reticulum	Columellae (µm)	Aperture Type	Plate
A. asteroides	Hedlund and Norris 1968	16-24	(sub)circular	columellate, semitectate 1.3-1.9	0.6-1.0	0.5-0.7	-	densely spaced head Ø 0.4-0.6	tri- to penta chotomo colpate	Plate I, Fig. 3-4
A. aff. *asteroides*	Hedlund and Norris 1968	~21	circular	columellate, semitectate 1.1	0.5-0.7	0.4-0.6	-	widely spaced head Ø 0.4	hexachotomo colpate	Plate I, Fig. 5-6
A. sp. 3	Heimhofer et al. 2007	~25	circular	columellate, semitectate 1.3	1.0	0.3	perforate	very densely spaced head Ø 0.4	tri- to penta chotomo colpate	Plate I, Fig. 7
A. sp. 2	Heimhofer et al. 2007	19-28	(sub)circular	columellate, semitectate 1.4-1.5	0.8-1.0	0.5-0.7	-	widely spaced head Ø 0.5	trichotomo colpate	Plate I, Fig. 8-9

Genus *Clavatipollenites* Couper 1958

Species	Author	Size (µm)	Amb/ Shape	Exine (µm)	Sexine (µm)	Nexine (µm)	Reticulum	Columellae (µm)	Aperture Type	Plate
C. sp. A	Doyle and Robbins 1977	18-26	(sub)circular - elliptical	columellate, semitectate 1.5-2.0	0.9-1.5	0.6-0.8	-	very widely spaced head Ø 0.6-1.0	monocolpate	Plate I, Fig. 10-11
C. hughesii	Couper 1958	19-30	(sub)circular - elliptical	columellate, semitectate 1.0-1.8	0.6-1.4	0.5-1.0	-	densely spaced head Ø 0.5-1.0	monocolpate	Plate I, Fig. 14-15
C. sp. 1	Brenner 1963	14-16	(sub)circular	columellate, semitectate 1.5-1.9	1.0	0.9	-	widely spaced head Ø 0.5	monocolpate	Plate I, Fig. 12-13
C. sp. 2	Heimhofer et al. 2007	20-30	(sub)circular - elliptical	columellate, semitectate 0.5-1.5	0.4-0.8	0.2-0.6	perforate	densely spaced head Ø 0.2-0.4	monocolpate	Plate I, Fig. 16
C. tenellis	Phillips and Felix 1971	20-30	(sub)circular	columellate, semitectate 1.5-2.5	0.7-1.5	0.5-1.5	-	densely spaced head Ø 0.5-0.7	indistinct	Plate II, Fig. 1-2

Genus *Cretacaeiporites* Herngreen 1973

Species	Author	Size (µm)	Amb/ Shape	Exine (µm)	Sexine (µm)	Nexine (µm)	Reticulum	Columellae (µm)	Aperture Type	Plate
C. aff. *polygonalis*	Herngreen 1973	~20	(sub)circular	reticulate-semitectate 1.2	0.7	0.5	scabrate-granulate	densely spaced barely visible	polyporate	Plate II, Fig. 3
C. aff. *scabratus*	Herngreen 1973	~20	(sub)circular	columellate, semitectate 1.0	0.8	0.3	perforate	densely spaced head Ø 0.4	polyporate	Plate II, Fig. 4
C. sp. 1	Informal species	19-23	(sub)circular	reticulate-semitectate 1.7-2.4	1.0-1.2	0.5-1.2	irregular homobrochate lumen size: 0.5-1.0	densely spaced head Ø 0.5	polyporate	Plate II, Fig. 5-6
C. sp. 2	Informal species	~20	(sub)circular	reticulate-semitectate ~1.8	1.0-1.2	0.7	irregular heterobrochate lumen size: 0.5-2.5	widely spaced head Ø 0.8 muri verrucate through overtopping columellae	polyporate	Plate II, Fig. 7-9
C. sp. 3	Informal species	~16	(sub)circular	reticulate-semitectate 0.7	0.3	0.4	very finely striate	striae densely spaced head Ø 0.3	polyporate	Plate II, Fig. 10-11
C. sp. 4	Informal species	15-18	(sub)circular	reticulate-semitectate 0.9	0.4	0.3	perforate-scabrate	densely spaced barely visible	polyporate	Plate II, Fig. 12-13

Genus *Dichastopollenites* May 1975

Species	Author	Size (µm)	Amb/ Shape	Exine (µm)	Sexine (µm)	Nexine (µm)	Reticulum (µm)	Muri width (µm) & supra-tectal ornamentation	Columellae (µm)	Aperture Type	Plate
D. dunveganensis	Singh 1983	30-45	elliptical	reticulate-semitectate	-	-	heterobrochate lumen size: 3.0-12.0	0.8-1.3	widely spaced head Ø 0.9-1.0	zonosulcate	Plate II, Fig. 14
D. reticulatus	May 1975	19-30	(sub)circular - elliptical	reticulate-semitectate 1.7-2.7	1.2-2.0	0.3-0.7	homobrochate lumen size: 1.0-3.5*	0.8-1.4	widely spaced head Ø 0.4-0.8	zonosulcate	Plate II, Fig. 15-16
D. sp. 1	Informal species	22-27	(sub)circular	reticulate-semitectate 1.4-1.7	1.0-1.5	0.3	heterobrochate lumen size: 0.4-3.6*	~0.3	widely spaced head Ø 0.9	zonosulcate	Plate II, Fig. 17-18
D. sp. 4	Heimhofer et al. 2007	30-50	(sub)circular - elliptical	reticulate-semitectate 3.0-3.5	2.0-2.5	0.6-1.0	irregular heterobrochate meandering muri	~1.0	widely spaced head Ø 1.0	zonosulcate	Plate III, Fig. 1-2
D. sp. 5	Heimhofer et al. 2007	~23	elliptical	reticulate-semitectate 2.0	1.0-1.5	0.5	irregular heterobrochate meandering muri	0.5-0.6	widely spaced head Ø 0.7	zonosulcate	Plate III, Fig. 3-4
D. sp. 6	Heimhofer et al. 2007	25-50	(sub)circular - elliptical	reticulate-semitectate 2.8	2.0	0.8	irregular heterobrochate meandering muri	0.5-0.8 muri verrucate through overtopping columellae	widely spaced head Ø 0.5-1.0	zonosulcate	Plate III, Fig. 5-7

*sometimes with small (<1.0 µm) additional luminae adjacent to larger lumen

Genus *Hammenia* Hedlund and Norris 1968

Species	Author	Size (μm)	Amb/ Shape	Exine (μm)	Sexine (μm)	Nexine (μm)	Reticulum (μm)	Columellae (μm)	Aperture Type	Plate
H. sp. A	Burger 1993	~23	(sub)circular	columellate, semitectate 1.5	0.4	1.1	perforate lumen size: <0.3	widely spaced head Ø 0.6	hexa-aperturate	Plate III, Fig. 8-9

Genus *Penetetrapites* Hedlund and Norris 1968

Species	Author	Size (μm)	Amb/Shape	Exine	Reticulum	Aperture Type	Plate
P. mollis	Hedlund and Norris 1968	~22	(sub)circular - triangular	reticulate-semitectate	perforate-scabrate	three lentular equatorial apertures with a fourth aperture developed at one pole	Plate III, Fig. 10-11

Genus *Pennipollis* Friis, Pedersen and Crane 2000

Species	Author	Other publications	Size (μm)	Amb/ Shape	Exine (μm)	Sexine (μm) detached	Nexine (μm)	Reticulum (μm)	Muri width (μm) & supra-tectal ornamentation	Aperture Type	Plate
P. peroreticulatus	(Brenner 1963) Friis et al. 2000	-	~15	(sub)circular	reticulate-semitectate 1.5 acolumellate	1.0	0.5	heterobrochate lumen size: 1.0-3.7°	0.7 single row verrucae	monocolpate	Plate III, Fig. 12-13
P. reticulatus	(Brenner 1963) Friis et al. 2000	-	15-17	(sub)circular	reticulate-semitectate 1.0-2.0 acolumellate	1.0-1.5	0.5-1.0	homobrochate lumen size: 0.5-2.3	0.5-0.7 single row verrucae	monocolpate	Plate III, Fig. 14-15
P. sp. 1	Informal species	Retimono-knobble (Penny 1992)	~20	(sub)circular	reticulate-semitectate 2.8 acolumellate	1.8-2.2	0.6-1.0	heterobrochate lumen size: 1.5-2.6	0.5 densely verrucated	monocolpate	Plate III, Fig. 16-17
P. sp. 2	Informal species	-	20-27	(sub)circular	reticulate-semitectate 2.0-2.3 acolumellate	1.0-1.5	0.5-0.8	homobrochate lumen size: 1.5-4.0	0.3 no ornamentation	monocolpate	Plate III, Fig. 18-19

° lumen smaller near colpus

Genus *Phimopollenites* Dettmann 1973

Species	Author	Size (μm)	Amb/ Shape	Exine (μm)	Sexine (μm)	Nexine (μm)	Reticulum (μm)	Muri width (μm)	Columellae (μm)	Aperture Type	Plate
P. sp. 1	Informal species	~20	prolate to subcircular	reticulate-semitectate 1.1	0.6	0.4	homobrochate lumen size: 0.8-1.2	0.4	widely spaced head Ø 0.4	Tricolpate wide aperture	Plate IV, Fig. 1-2

Genus *Retimonocolpites* Pierce 1961

Species	Author	Size (μm)	Amb/ Shape	Exine (μm)	Sexine (μm)	Nexine (μm)	Reticulum (μm)	Muri width (μm) & supra-tectal ornamentation	Columellae (μm)	Aperture Type	Plate
R. dividuus	Pierce 1961	25-30	(sub)circular - elliptical	reticulate-semitectate 1.0-1.5	0.5-1.0	0.3-0.5	homobrochate lumen size: 0.5-1.5	0.3	densely spaced head Ø 0.4-0.6	monocolpate elongate colpus	Plate IV, Fig. 3-4
R. aff. *dividuus*	Pierce 1961	12-22	(sub)circular	reticulate-semitectate 1.6-2.3	0.8-1.4	0.6-1.0	homobrochate lumen size: 0.7-1.6	0.2	densely spaced head Ø 0.5-0.7 club shaped	monocolpate elongate colpus	Plate IV, Fig. 5-6
R. sp 1	Informal species	~15	(sub)circular	reticulate-semitectate 1.6	1.0	0.6	homobrochate loosely attached very fine meshwork <1.0	<0.4	widely spaced head Ø 0.3	monocolpate	Plate IV, Fig. 7-8
R. sp. 2	Informal species	20-27	(sub)circular - elliptical	reticulate-semitectate 1.6-2.0	0.7-1.5	0.5-1.0	heterobrochate lumen size: 0.5-3.5	0.3 muri verrucate through overtopping columellae	widely spaced head Ø 0.7-1.4	monocolpate	Plate IV, Fig. 9-10
R. sp. 3	Informal species	19-23	(sub)circular	reticulate-semitectate 1.6-2.0	1.0-1.2	0.5-0.8	homobrochate lumen size: <1.0	0.2-0.4	densely spaced head Ø 0.4	monocolpate	Plate IV, Fig. 11-12
R. sp. 4	Informal species	~20	(sub)circular	reticulate-semitectate 1.8-2.2	1.4	0.8	irregular heterobrochate meandering muri	~0.5	widely spaced head Ø 1.0-1.3	monocolpate	Plate IV, Fig. 13-14
R. sp. 5	Heimhofer et al. 2007	~30	prolate	reticulate-semitectate 1.6-1.8	0.9	0.8	heterobrochate lumen size: 0.6-1.4	0.5	densely spaced head Ø 0.7 club shaped	monocolpate	Plate IV, Fig. 15
R. sp.6	Informal species	19-22	(sub)circular - elliptical	reticulate-semitectate 2.8	1.5-2.0 loosely attached	0.8-1.0	heterobrochate lumen size: 0.4-3.2°	0.5-0.6 muri verrucate through overtopping columellae	widely spaced head Ø 0.5-0.8	monocolpate	Plate IV, Fig. 18-20
R. sp. 7	Informal species	27	elliptical	reticulate-semitectate 1.7	1.3	0.4	homobrochate lumen size: 1.4-1.8	0.3 muri verrucate through overtopping columellae	densely spaced head Ø 0.6	monocolpate	Plate IV, Fig. 16-17

° lumen smaller near colpus

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Genus *Retitrescolpites* Sah 1967

Species	Author	Size (μm)	Amb/ Shape	Exine (μm)	Sexine (μm)	Nexine (μm)	Reticulum (μm)	Muri width (μm)	Columellae (μm)	Aperture Type	Plate
R. sp. 1	Informal species	19-23	(sub)circular	reticulate-semitectate 2.0-2.9	1.5-1.8	0.5-0.8	homobrochate lumen size: 0.5-3.0	0.4-0.7	widely spaced head Ø 0.7	tricolpate	Plate V, Fig. 1-2
?*R.* sp. 2	Informal species	18-24	(sub)circular	reticulate-semitectate 2.6	2.0*	0.6	irregular homobrochate lumen size: 0.8-2.0	0.7-1.0	widely spaced head Ø 0.6	tricolpate long colpi, bordered by 2 μm thick margo	Plate V, Fig. 3-4
R. sp. 3	Informal species	~21	(sub)circular	reticulate-semitectate ~1.6	1.0-1.2	0.5	homobrochate lumen size: 1.0-1.3	0.3	widely spaced head Ø 0.6 club shaped	tricolpate short colpi	Plate V, Fig. 5-6
?*R.* sp. 4	Informal species	~25	(sub)circular	reticulate-semitectate 4.0-5.0	3.1-4.5* loosely attached	0.5-0.9	homobrochate lumen size: 3.7-5.0	0.6	widely spaced head Ø 0.8	tricolpate	Plate V, Fig. 7-8
R. sp. 5	Informal species	~17	(sub)circular	reticulate-semitectate 3.0	2.0	1.0	homobrochate lumen size: 1.2-1.8	0.8-1.0	widely spaced head Ø 1.0	tricolpate	Plate V, Fig. 9-10
R. sp. 6	Informal species	~23	(sub)circular	reticulate-semitectate 1.5	1.0	0.5	homobrochate lumen size: 1.3-2.1	0.4	widely spaced head Ø 0.5	tricolpate	Plate V, Fig. 11

* detached sexine

Genus *Rousea* Srivastava 1969

Species	Author	Size (μm)	Amb/ Shape	Exine (μm)	Sexine (μm)	Nexine (μm)	Reticulum (μm)	Muri width (μm)	Columellae (μm)	Aperture Type	Plate
R. georgensis	Brenner 1963	~25-28	prolate - oblate	reticulate-semitectate 1.5-1.7	1.3	0.4	heterobrochate lumen size: 0.3-2.2°	0.3-0.5	densely spaced head Ø 0.4 club shaped	tricolpate	Plate V, Fig. 12-13
R. aff. *prosimilis*	Norris 1967	~20	(sub)circular	reticulate-semitectate 2.0-3.0	1.5-2.2*	0.6-0.8	heterobrochate lumen size: 0.5-3.0°	0.4-0.7	widely spaced head Ø 0.7	tricolpate	Plate V, Fig. 14-15
R. prosimilis	Norris 1967	~18-26	prolate	reticulate-semitectate 1.0	0.7	0.3	irregular heterobrochate lumen size: 0.2-2.1	0.3	densely spaced head Ø 0.4 club shaped	tricolpate	Plate VI, Fig. 9-10
R. sp. 1	Informal species	17-24	prolate	reticulate-semitectate 1.5	1.0	0.5	heterobrochate lumen size: 0.3-1.8+	0.3	widely spaced head Ø 0.7	tricolpate	Plate V, Fig. 16-17
?*R.* sp. 2	Informal species	20-26	prolate	reticulate-semitectate 2.0-2.6	1.6-2.0*	0.6	heterobrochate lumen size: 0.5-3.8 loosely attached	0.4-0.6 muri verrucate through overtopping columellae	widely spaced head Ø 0.8	tricolpate	Plate V, Fig. 18-19
R. sp. 3	Informal species	20-23	(sub)circular	reticulate-semitectate 1.2	0.6	0.6	irregular heterobrochate small lumen between larger 0.2-1.7+	~0.5	widely spaced head Ø 0.3	tricolpate	Plate V, Fig. 20 Plate VI, Fig. 1
?*R.* sp. 4	Informal species	~22	(sub)circular	reticulate-semitectate 1.8	1.2*	0.7	irregular heterobrochate lumen size: 0.7-4.0	0.3-0.5	widely spaced head Ø 0.5	tricolpate	Plate VI, Fig. 2-4
?*R.* sp. 5	Informal species	~22	oblate	reticulate-semitectate 3.0	2.6*	0.4	heterobrochate lumen size: 0.5-2.5°	0.3 muri verrucate trough overtopping columellae	widely spaced head Ø 0.5	tricolpate	Plate VI, Fig. 5-6
?*R.* sp. 6	Informal species	~17	(sub)circular	reticulate-semitectate 1.4	1.0	0.4	irregular heterobrochate lumen size: 0.7-1.8	0.3 muri verrucate through overtopping columellae	widely spaced head Ø 0.5	tricolpate broad colpi	Plate VI, Fig. 7-8
R. sp. 7	Informal species	~27	(sub)circular	reticulate-semitectate 2.2	1.5-1.6	0.6-0.8	heterobrochate lumen size: 0.4-1.6°	0.5 muri verrucate through overtopping columellae	widely spaced head Ø 0.9 club shaped	tricolpate	Plate VI, Fig. 11-12
R. sp. 8	Informal species	16-18	(sub)circular	reticulate-semitectate 2.5-2.7	1.8-2.0	0.7	heterobrochate lumen size: 1.0-3.3	0.8 muri verrucate through overtopping columellae	densely spaced head Ø 0.4-0.6	tricolpate	Plate VI, Fig. 13-14

* detached sexine

° lumen smaller near colpus

+ lumen smaller near pole

Genus *Senectotetradites* Dettmann 1973

Species	Author	Size (μm)	Amb/ Shape	Exine (μm)	Sexine (μm)	Nexine (μm)	Reticulum (μm)	Muri width (μm)	Columellae (μm)	Aperture Type	Plate
S. varireticulatus	Dettmann 1973	40-44 (tetrad) 22-32 (grain)	prolate to oblate	columellate, semitectate 1.8-2.8	1.3-2.5	0.5-1.0	heterobrochate Lumen size: 1.3 at pole: 3.0 at equator	0.6	densely spaced head Ø 0.9	tricolpate	Plate VI, Fig. 15-16

Genus *Stellatopollis* Doyle, van Campo and Lugardon 1975

Species	Author	Size (μm)	Amb/Shape	Exine	Aperture Type	Plate
S. barghoornii	Doyle et al. 1975	~50	elliptical	reticulate-semitectate, supratectal elements with elevated triangular elements, arranged around a circular area	monocolpate	Plate VI, Fig. 17
S. sp. 1	Informal species	~17 (fragment)	unknown (broken)	reticulate-semitectate, supratectal elements irregular shaped, with elevated mostly oval elements, arranged around a circular area (only fragment found)	monocolpate	Plate VI, Fig. 18-19

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Genus *Striatopollis* Krutzsch 1959

Species	Author	Size (µm)	Amb/ Shape	Exine (µm)	Sexine (µm)	Nexine (µm)	Reticulum (µm)	Columellae (µm)	Aperture Type	Plate
S. paraneus	Norris 1967	~18-28	prolate	striato-reticulate 1.0	0.8	0.2	striate striae often running oblique to colpus	densely spaced head Ø 0.5	tricolpate	Plate VI, Fig. 20-21
S. trochuensis	Srivastava 1967 Ward 1986	~20	(sub)circular	striato-reticulate 1.1	0.5-0.8	barely visible	striate	widely spaced head Ø 0.4	tricolpate	Plate VI, Fig. 22 Plate VII, Fig. 1-2
S. vermimurus	Srivastava 1977	~17-23	(sub)circular	striato-reticulate 1.7	1.1	0.6	irregular heterobrochate lumen size: 0.3-1.7	widely spaced head Ø 0.5	tricolpate	Plate VII, Fig. 3-5
S. sp. 1	Informal species	19-25	(sub)circular	striato-reticulate 2.5	1.0-2.3	0.5	irregular heterobrochate	widely spaced head Ø 0.6 muri verrucate through overtopping columellae	tricolpate	Plate VII, Fig. 6-7
S. sp. 2	Informal species	25-27	prolate	striato-reticulate 1.3-1.7	1.0-1.4	0.3	irregular heterobrochate lumen circular shaped max 2.5 near equator	irregular spaced head Ø 0.7	tricolpate	Plate VII, Fig. 8-10
S. sp. 3	Informal species	~22	prolate	striato-reticulate 4.0	3.5-3.8	0.5	striate	densely spaced head Ø 0.6	tricolpate	Plate VII, Fig. 11-12
S. sp. 4	Informal species	~20	(sub)circular	striato-reticulate 1.2-1.3	1.2	barely visible	irregular heterobrochate lumen max 1.4 near equator	widely spaced head Ø 0.4	tricolpate	Plate VII, Fig. 13
S. sp. 5	Informal species	~22	(sub)circular	striato-reticulate 1.3-1.5	0.9-1.3	0.3	irregular heterobrochate lumen size < 1.0	densely spaced head Ø 0.6 striae short	tricolpate	Plate VII, Fig. 14-15
S. sp. 6	Informal species	~20	prolate	striato-reticulate 2.0-4.0	2.0-3.5	0.5	striate	densely spaced head Ø 0.3	tricolpate	Plate VII, Fig. 16-18

Tetracolpate form

Species	Author	Size (µm)	Amb/ Shape	Exine (µm)	Sexine (µm)	Nexine (µm)	Reticulum (µm)	Muri width (µm)	Columellae (µm)	Aperture Type	Plate
Tetracolpate form 1	Informal species	~17	circular	reticulate-semitectate 1.0	0.7	0.3	homobrochate lumen size: 0.5-0.8	0.6	densely spaced head Ø 0.5 club shaped	Tetracolpate	Plate VII, Fig. 19-20

Genus *Tricolpites* Cookson ex Couper, 1953

Species	Author	Size (µm)	Amb/ Shape	Exine (µm)	Sexine (µm)	Nexine (µm)	Reticulum (µm)	Muri width (µm)	Columellae (µm)	Aperture Type	Plate
T. aff. *albiensis*	Kemp 1968	12-15	(sub)circular	reticulate-semitectate 0.7	0.5	0.2	homobrochate lumen size: 0.4-0.9	0.2-0.3	widely spaced head Ø 0.3	tricolpate	Plate VIII, Fig. 1-2
T. blechrus	Ward 1983	~17	(sub)circular	reticulate-semitectate 1.3	0.8	0.5	homobrochate lumen size: < 0.8	0.4	widely spaced head Ø 0.6 club shaped	tricolpate	Plate VIII, Fig. 3-4
T. crassimurus	(Groot and Penny) Singh 1971	~32	prolate	reticulate-semitectate 1.6	1.0	0.5	perforate <0.3	0.6	densely spaced head Ø 0.4	tricolpate	Plate VIII, Fig. 5-7
T. aff. *fragosus*	(Hedlund and Norris 1968) Ward 1986	18-22	(sub)circular	reticulate-semitectate 0.8-1.3	0.4-0.6	0.4-0.8	heterobrochate lumen size: <0.2 at equator: 0,9 at pole	0.3	densely spaced head Ø 0.2	tricolpate	Plate VIII, Fig. 8-10
T. sagax	Norris 1967	~24	(sub)circular	reticulate-semitectate 1.0	0.7	barely visible < 0.2	perforate-scabrate	barely visible	densely spaced barely visible	tricolpate	Plate VIII, Fig. 11
T. vulgaris	Srivastava 1969	~24	(sub)circular	reticulate-semitectate 1.2	0.8	0.4	homobrochate lumen size: 0.5-0.6	0.3-0.4	densely spaced head Ø 0.4 club shaped	tricolpate	Plate VIII, Fig. 12-14
T. sp. 1	Informal species	~19	(sub)circular	reticulate-semitectate 1.5	1.0	0.5	heterobrochate lumen size: <0.2 at equator: 0,9 at pole	0.4	widely spaced head Ø 0.4	tricolpate	Plate VIII, Fig. 15-16

Tricolporate form

Species	Author	Size (µm)	Amb/ Shape	Exine (µm)	Sexine (µm)	Nexine (µm)	Reticulum (µm)	Muri width (µm)	Columellae (µm)	Aperture Type	Plate
Tricolporate form 1	Informal species	~20	oblate	striato-reticulate 2.3	1.5 (detached)	0.8	striate	0.3	densely spaced head Ø 0.3	Tricolporate	Plate VIII, Fig. 17-18
Tricolporate form 2	Informal species	21	oblate	reticulate-semitectate 1.4 thicker along colpi	1.0 (detached)	0.4	perforate < 0.6	0.4	widely spaced head Ø 0.6	Tricolporate	Plate VIII, Fig. 19-20
Tricolporate form 3	Informal species	19	oblate	reticulate-semitectate 1.4	1.0	0.4	heterobrochate lumen size: 0.2-1.7°	0.4	densely spaced head Ø 0.3	Tricolporate (invaginated)	Plate VIII, Fig. 21-22

°lumen smaller near colpus

Triporate form

Species	Author	Size (µm)	Amb/ Shape	Exine (µm)	Sexine (µm)	Nexine (µm)	Reticulum (µm)	Muri width (µm)	Columellae (µm)	Aperture Type	Plate
Triporate form 1	Informal species	26	(sub)circular	reticulate-semitectate	0.6	0.6 slightly thicker near pores	irregular heterobrochate lumen size: 0.6-1.4	0.3	densely spaced head Ø 0.4	Triporate	Plate VIII, Fig. 23-24

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